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Biodiversity patterns and their conservation in wetlands of the Western Australian wheatbelt

S.A. Halse[1], M.N. Lyons[1], A.M. Pinder[1] and R.J. Shiel[2]
[1]Department of Conservation and Land Management, Science Division,
P.O. Box 51 Wanneroo, Western Australia 6946, Australia
[2]Department of Environmental Biology, University of Adelaide, South Australia 5005, Australia

Abstract – A total of 197 wetlands were sampled between 1997 and 2000 in a survey designed to record wetland biodiversity across the wheatbelt and south coast of Western Australia, an area of 205 000 km^2. Altogether, 986 wetland-associated plant, 844 aquatic invertebrate and 57 waterbird species were recorded, with an average of 73 and a range of 10–174 species per wetland. Thirty-four per cent of species were found at only one wetland.

Sixteen types of wetland were recognized, based on their biological assemblages. Overall, salinity was the factor most responsible for differentiation between wetlands in terms of biodiversity but differences between some freshwater wetland types, such as sedge swamps and granite rock pools, were largely attributable to other abiotic factors. Among saline wetlands, the biota of naturally saline (and usually very salty) seasonal playas was distinct from that of wetlands with longer periods of inundation. It was unclear whether differences related to inundation or salinity.

Using cluster analysis, 22 assemblages of co-occurring species were identified and the distributions of 18 of them were modelled. Between 33 and 86% of the species richness of each assemblage at a wetland was explained by two to four abiotic variables. The assemblages that modelled most poorly consisted of species that were widespread and had broad ecological tolerances, with ranges extending beyond the wheatbelt, so that the survey was unlikely to have circumscribed their ecological requirements. Most assemblages consisted of a mix of plant, invertebrate and (fewer) waterbird species. Factors affecting the distribution of plants and animals within a co-occurring assemblage often appeared to differ, especially for plants growing on the bank of a wetland. Riparian plants are probably exposed to different environmental factors, especially salinity patterns, than those influencing animals using the waterbody itself.

The dramatic increase in secondary salinisation that has been observed in the wheatbelt and south coast over the past 100 years, with associated loss of freshwater habitat and changes to naturally saline playas, is likely to lead to significant loss of biodiversity. Most assemblages (and species) were associated with particular salinity ranges and there was an inverse relationship between overall community richness and salinity, especially within the waterbody. Many species typical of naturally saline playas were rarely found at secondarily saline wetlands.

The predictable occurrence of some species assemblages, such as those characteristic of sedge swamps and saline playas of the north-eastern wheatbelt, makes it possible to identify wetlands that, if protected from secondary salinisation, will conserve large proportions of them. Some other assemblages occur at many wetlands and their conservation is assured by almost any strategy, even if they are unpredictably distributed. However, protection of rare species and assemblages that occur infrequently and somewhat randomly within the wheatbelt poses a significant challenge to wetland managers.

INTRODUCTION

South-west Western Australia is an old, deeply weathered landscape with flat topography and large expanses of nutrient deficient soils (Mulcahy, 1967; Wyrwoll, 1988). The steep rainfall gradient with distance from the coast (Figure 1) means the extreme south-west supports wet sclerophyll forest and permanent wetlands while more inland areas contain open woodland or shrublands and episodically flooded waterbodies (Hopper, 1979; Beard, 1990).

This paper reports results of a biological survey

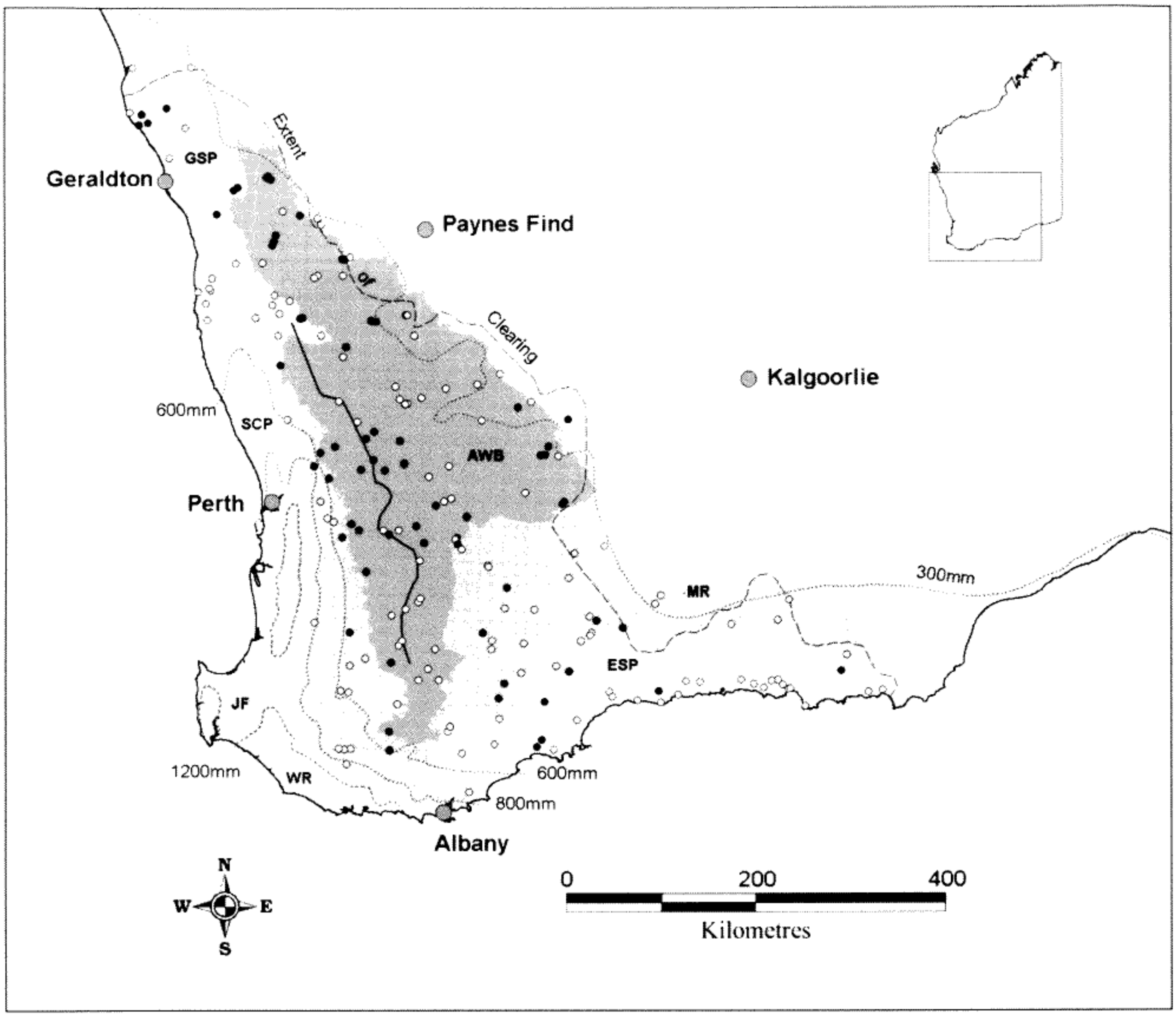

Figure 1 Wheatbelt and south coast of south-west Western Australia showing the wetlands surveyed, rainfall isohyets, IBRA regions (Thackway and Cresswell 1995), and the Meckering line (Mulcahy 1967). O, site on public land; ●, site on private land; GSP, Geraldton Sandplain; SCP, Swan Coastal Plain; AWB, Avon Wheatbelt; JF, Jarrah Forest; WR, Warren; ESP, Esperance Sandplain; MR, Mallee Region.

(WBS) of wetlands of the wheatbelt and south coast of Western Australia, with small incursions into adjacent forested or open woodland areas. Many wetlands in the surveyed area were saline. Salt has been accumulating in soil profiles and groundwaters of the wheatbelt for hundreds of thousands of years (Commander *et al.*, 1994) as the result of a higher rate of deposition of marine aerosol salt on the landscape than salt discharge via rivers and groundwater flow (Hingston and Gailitis, 1976). Consequently, most playa lakes formed by groundwater discharge were naturally saline (e.g. Salama, 1994), as were some river systems on the south coast. Even most 'freshwater' wetlands had relatively high salt levels by global standards prior to clearing of native vegetation (Schofield *et al.*, 1988). However, nowadays many of the saline wetlands in the surveyed area are salty because of secondary salinisation (Mulcahy, 1978; George *et al.*, 1995). The clearing of perennial native vegetation and its replacement with annual crops and pastures caused run-off and recharge to increase. As a consequence, groundwater levels have risen and salt previously stored in the soil profile, as well as in groundwater, has been mobilised and percolated to the surface (Clarke *et al.*, 2002). It has been estimated that about 6% of land in the surveyed area is currently salinised (groundwater within 2 m of surface) and that this will eventually increase to 33% (Short and McConnell, 2001; George *et al.*, 2002). The proportion of wetlands affected is much higher because of their low position in the landscape (Halse *et al.*, 1993b, 2000a).

Salinity is a major environmental gradient structuring aquatic communities (Hammer, 1986) and the historical prevalence of salt in wetlands of the surveyed area has resulted in an aquatic fauna that is relatively salt-tolerant (Williams *et al.*, 1991; Halse *et al.*, 2000a; Kay *et al.*, 2001; Pinder *et al.*, 2002). Likewise, there has been considerable radiation of salt-tolerant plant species in, and adjacent to, wheatbelt wetlands (Short, 1982; Wilson, 1984; Lyons *et al.*, 2004). Nevertheless, secondary salinisation has the potential to wreak devastating changes on the biodiversity of the wheatbelt because of loss of freshwater wetlands and the likely changes to temporal and spatial patterns of salinity in naturally saline wetlands (Williams, 1999; Cramer and Hobbs, 2002; Halse *et al.*, 2003).

The impact of salinisation in south-west Western Australia is made more acute by the region's high conservation values. The extensive radiation of vascular plant groups, especially the Myrtaceae, Proteaceae, Papilionaceae and Mimosaceae, has long been recognized (Diels, 1906; Beard *et al.*, 2000) and the south-west was listed by Myers *et al.* (2000) as one of 25 global hotspots for biodiversity, based on a combination of terrestrial (mainly plant) species richness and the extent of land clearing. Many high-conservation value, endemic plant species occur in high-rainfall areas (Wardell-Johnson and Horwitz, 1996) but the number is greater in what Hopper (1979) termed the 'intermediate rainfall zone' between 300–800 mm annual rainfall. This is the area covered by the WBS. Hopper (1979) attributed plant richness in the study area to the existence of a mosaic of soil types and the isolation brought about by climatic variability, mostly since the Quaternary.

The importance of south-west Western Australia for aquatic invertebrates is less well documented than for plants but it appears to be a region of significant richness and endemism for groups with drought-resistant eggs, especially crustaceans (Frey, 1991; Maly and Bayly, 1991; Thomsen, 1999). The distribution of crustaceans has parallels with plants: while many endemic species occur in areas of high rainfall (Storey *et al.*, 1993; Wardell-Johnson and Horwitz, 1996), much of the crustacean endemism occurs in intermediate and low rainfall zones (Halse and McRae, 2001; Remigio *et al.*, 2001; Halse, 2002; Timms, 2002).

The WBS was a direct response by the Government of Western Australia to the threat of broad-scale loss of biodiversity because of secondary salinisation (Anonymous, 1996b). It had three objectives: (1) to document patterns of biodiversity in wetlands of the wheatbelt and south coast, (2) to investigate the role of salinity and other environmental factors in structuring communities, and (3) to select a set of Natural Diversity Recovery Catchments as a focus for government and community actions to ameliorate the impact of salinity on biodiversity and thus conserve representative wetland communities. Existing information relevant to the three objectives is reviewed below.

Prior to the survey, there had been little investigation of biodiversity patterns in wetlands of the surveyed area other than for waterbirds (Jaensch *et al.*, 1988; Halse *et al.*, 1993b, 1995). Studies of invertebrates were limited to a few wetlands (Halse, 1981; Williams *et al.*, 1991; Doupé and Horwitz, 1995; Halse *et al.*, 2000a) or focussed on particular taxonomic groups (Geddes *et al.*, 1981; Brock and Shiel, 1983). The comprehensive survey of rivers by Kay *et al.* (2001) identified invertebrates only to family. Studies of submerged plants were few (Brock and Lane, 1983; Brock and Shiel,1983) and, other than the broadscale survey by Halse *et al.* (1993a), studies of emergent and riparian vegetation were restricted to particular wetlands (Froend *et al.*, 1987; Froend and McComb, 1991; Froend and van der Moezel, 1994). Substantially more information on plants and invertebrates, as well as diatoms, is available as a result of the WBS (Pinder *et al.*, 2000, 2002, 2004, 2005; Blinn *et al.*, 2004; Lyons *et al.*, 2004).

The general role of salinity in structuring plant and animal communities within a waterbody is reasonably well understood. While there is a trend for community richness to be inversely related to salinity, the affinity of different higher-level taxonomic groups for saline conditions varies (Hammer, 1986). These patterns were confirmed in the WBS with Pinder *et al.* (2005) showing a tight negative relationship between invertebrate richness and salinity at values >4 g L^{-1} across both secondarily and naturally saline wetlands. Waterbird and diatom richness also showed negative relationships with salinity (Blinn *et al.*, 2004; Cale *et al.*, 2004). The role of salinity in structuring riparian plant communities, especially those of naturally saline systems, is less clear (see Hart *et al.*, 1991). Halse *et al.* (1993a) found no relationship between plant species richness and natural salinity of wetlands, although secondary salinisation reduced richness. Lyons *et al.* (2004) reached similar conclusions, after comparing soil salinity and plant richness of small quadrats in various vegetation associations around wetlands during the WBS. Richness of riparian plants was poorly correlated with wetland salinity probably because the salt content of riparian soils reflects microscale topography and leaching rather than the salinity value of wetland water (Cramer and Hobbs, 2002).

The practice of reserving or managing areas to protect the biota within them, and thus the flora and fauna of the region, has a significant international history (Margules and Pressey, 2000). The first national park in Western Australia (John Forrest) was gazetted in 1900 but it was another 52 years before the first nature reserve was proclaimed

(Tammin Railway Dam). Between then and 1980, many wetlands within the surveyed area were reserved to provide habitat for waterfowl, as well as being places where ducks could be shot (Lane, 1985). Other wetlands were included in nature reserves where the primary purpose was protection of terrestrial flora and fauna. Early reservation was an *ad hoc* process but, in recent years, a number of relatively sophisticated mathematical methods have been developed in Australia, and elsewhere, to maximise the number of species from the regional species pool that are protected by reserving a given area. The focus of these methods has been terrestrial ecosystems (e.g. McKenzie *et al.*, 1989; Nicholls, 1989; Justus and Sarkar, 2002; Scotts and Drielsma, 2003) but many of the principles apply to wetland reservation. In conjunction with the development of analytical methods, there has been a program of regional surveys in Western Australia to provide the biological data on which to base decisions about reservation (Biological Survey Committee, 1984; McKenzie and Robinson, 1987; McKenzie *et al.*, 1991, 2000), with aquatic ecosystems being included in these surveys since the mid-1990s (Halse *et al.*, 2000b).

Selection of Natural Diversity Recovery Catchments (BRCs) to ameliorate impact of salinity on biodiversity uses the same information as a reserve selection process. There are currently six BRCs in south-west Western Australia (Figure 2). Each BRC is a sub-catchment of 50 000 – 120 000 ha with several or many wetlands at low points within the catchment. All contain a small number of nature reserves, and some remnant vegetation on freehold land, but much of each catchment is cleared agricultural land. Public money is being spent within these catchments on salinity control, revegetation and management of uncleared land with the objective of maintaining existing levels of biodiversity. At the Toolibin BRC, groundwater is

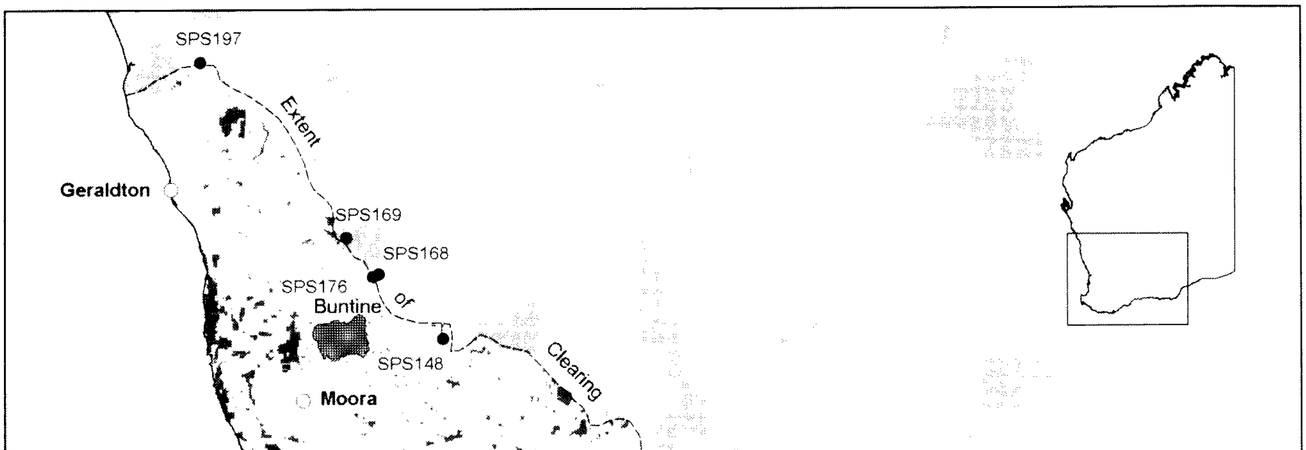

Figure 2 Wheatbelt and south coast of south-west Western Australia showing existing Natural Diversity Recovery Catchments (hatched), major nature reserves and the Potential Recovery Wetlands selected as a result of the survey. ● PRW.

being pumped from under Toolibin Lake to lower the water-table and maintain health of the lake vegetation (Froend *et al.*, 1997; Dogramaci, 2003). It is intended that an additional 10-20 BRCs will be selected and that most of the species assemblages identified in the WBS will be protected in these catchments (see Anonymous, 1996a; Keighery, 2001).

STUDY AREA

The area covered by the WBS is shown in Figure 1. Nearly all wetlands were located between the 600 and 300 mm isohyets. The area has a Mediterranean climate with hot dry summers and predominantly winter rainfall, although the proportion of summer rain increases with distance to the north and east (Gentilli, 1972). Annual evaporation varies from 1320 to 2750 mm. Rainfall was relatively light, and wetland levels low, during 1997 and 1998 (Figure 3). Extensive late summer and autumn rains in 1999 meant that wetlands remained extensively flooded throughout that year. Rainfall patterns within the surveyed area during 2000 were similar to 1997 and 1998, although there was extensive rain farther east.

The different landforms and vegetation associations of the surveyed area are reflected in the IBRA regions it covers. The boundaries of these regions largely reflect geology and vegetation formations (Thackway and Cresswell, 1995). Most of the wetlands surveyed are in the Avon Wheatbelt, Esperance Sandplains and Geraldton Sandplains regions, with a small number in the Mallee and Jarrah Forest. Lake Cronin (SPS003) is in the Coolgardie region. In broad terms, the natural vegetation of the Geraldton and Esperance Sandplains consists of shrublands, the Avon Wheatbelt contains open eucalypt woodlands and the Mallee contains eucalypt mallee formations (Gibson *et al.*, 2004). However, surrounding plant formations have relatively little influence on plant species occurring within the regularly inundated parts of wetlands. It must also be recognized approximately 90% of the Avon-Wheatbelt, 80% of the Mallee, 73% of the Geraldton Sandplains and 55% of the Esperance Sandplains have been cleared of their original vegetation during the past 100 years (Shepherd *et al.*, 2001), with broad-acre cropping now the main activity.

Physiognomy and patterns of inundation of wetlands in the surveyed area are highly variable. No wetland is permanently filled, although some of the deeper wetlands in the most south-westerly part of the surveyed area, around Lake Muir, rarely dry. West of the Meckering line (Figure 1) and along the south coast, rivers have defined channels, flow seasonally for several months and usually dry during summer. Farther inland, drainage lines consist of broad palaeochannels that are rarely connected to active rivers and contain mosaics of flat channels and small playas (Mulcahy, 1967; Beard, 1999). They contain water only briefly after large rainfall events. Lentic waterbodies include semi-permanent or seasonal basin wetlands, often with rivers flowing into and out of them that may connect a series of wetlands, such as Lake Toolibin on the northern Arthur River (Froend *et al.*, 1997). Most basin wetlands are in the western and southern parts of the surveyed area. In higher rainfall zones, the bed is usually covered by sedges while lower rainfall results in trees growing across the bed unless the centre of the wetland remains water-logged for prolonged periods (as often occurs), when it will be open (Halse *et al.*, 1993a). Shrubs such as *Muehlenbaeckia* spp. sometimes occur instead of trees in wetlands of low rainfall zones.

Other lentic wetland types include seasonally or episodically filled playa lakes. These are more common in the eastern part of the surveyed area and vary in size from a few 100 m^2 to several 100 km^2. Many are naturally saline and support lunettes on the downwind side (Bowler, 1983) with vegetation in low-lying areas around the wetland margin consisting mostly of chenopods. Playa lakes are maintained as landscape features by groundwater discharge (Salama, 1994; Harper and Gilkes, 2003) but most fill only after surface or sub-surface inflow.

A variety of vernal pools, claypans and pools on granite outcrops also occur. Vernal pools are perched above regional water-tables, usually on impervious clay sediments, and seasonally contain shallow water for a few months. They are fed by surface run-off from their immediate catchment and support dense stands of sedges and small shrubs across the wetland. They form only in areas of moderately high rainfall and occur mostly on the western edge of the surveyed area. Claypans are analogous to vernal pools, occurring in low rainfall areas in the eastern part of the surveyed area. When flooded they contain either open water (often very turbid) or emergent plants, such as *Tecticornia verrucosa, Muehlenbaeckia florulenta* and *Eragrostis australasica*. Granite rock pools have been comparatively well studied (Hopper *et al.*, 1997; Bayly, 1999; Pinder *et al.*, 2000). They occur in small depressions on inselbergs and share many similarities with vernal pools although, because of their rock substrate, they usually do not support emergent vegetation.

The surveyed area extended to both the south and west coasts (Figure 1) and, near the coastlines, saline lakes of marine origin are present. These are either part of old estuary systems or shallow lakes in inter-dunal swales (Hodgkin and Hesp, 1998). They usually support extensive chenopd marshes on their margins and sometimes stands of salt-tolerant *Melaleuca cuticularis*.

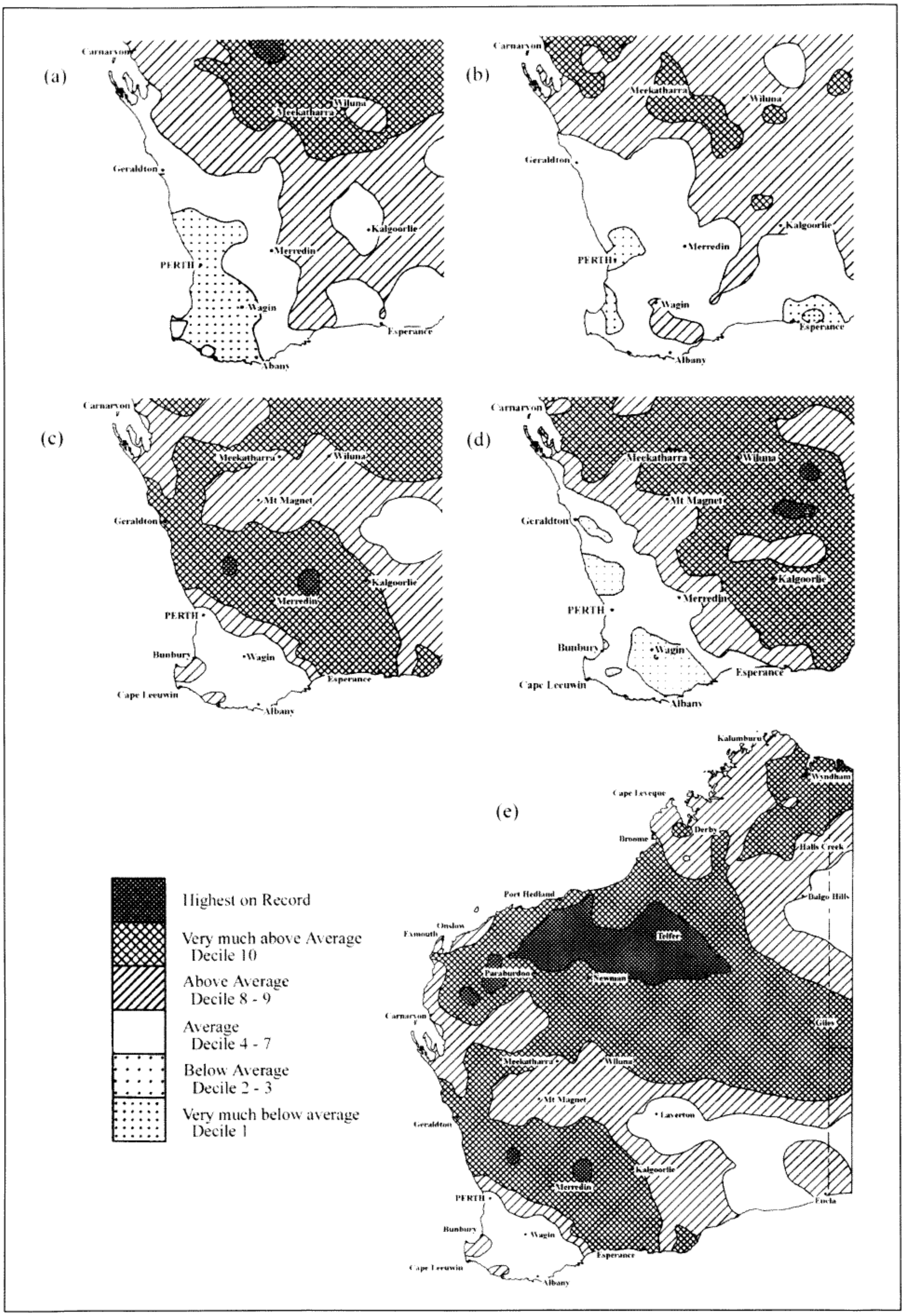

Figure 3 Rainfall deciles in the surveyed area during 1997–2000, and rainfall over all Western Australia during 1999. (a) 1997, (b) 1998, (c) 1999, (d) 2000, (e) whole State in 1999 (data from Bureau of Meteorology).

Secondary salinisation has already affected many wetlands of the surveyed area. The most visible effects are increased inundation, increased salinity, and death of lake-bed and riparian vegetation (Cramer and Hobbs, 2002; Halse *et al.*, 2003)

METHODS

This paper is based data from 197 wetlands (Figure 1, Appendix 1), which are a subset of those surveyed for plants by Lyons *et al.* (2004) and aquatic invertebrates by Pinder *et al.* (2004). Dams, reservoirs and wetlands receiving hypersaline discharge water were excluded from our analysis, which dealt only with naturally occurring wetlands. Most of these were on Crown land (nature, water or recreation reserves or unvested) but 65 were on freehold land, which had usually been cleared for agriculture except for a narrow belt of riparian vegetation, and seven were on pastoral leases. Many wetlands in reserves also had little uncleared land around them and in some cases the reserved area did not encompass the whole wetland (see Halse *et al.*, 1993a).

The WBS examined patterns in composition and distribution of the overall biological communities in wetlands, as represented by three elements with different life history traits: namely waterbirds, aquatic invertebrates, and vascular plants within the wetland and riparian zone. We define the riparian zone as extending to the high-water mark of major, regular (though not necessarily annual) flood events. Aquatic invertebrates and waterbirds in wetlands of the central third of the study area were surveyed in spring 1997, the southern third in spring 1998 and the northern third in spring 1999 (Pinder *et al.*, 2004). Four additional wetlands were surveyed in 2000. Wetlands of southern and some central parts of the study area were surveyed for plants in 1998 and those in northern and the remaining central parts were sampled in 1999 with spring and summer visits to each wetland to coincide with periods of maximal flowering activity (Lyons *et al.*, 2004). Five wetlands were surveyed in 2000.

There was temporal disparity between the animal and plant data-sets for many wetlands, including all those sampled for fauna in 1997. Conditions did not change much between animal and plant sampling if both occurred in 1997 and 1998, because these years had similar rainfall patterns (Figure 2), but differences were sometimes marked if plants were sampled in 1999 and animals during the preceding two years. We have been unable to compensate for temporal discrepancies except for seven wetlands in the data-set of Pinder *et al.* (2004) that were sampled twice, in different years. For these, faunal data were used from the year when wetland conditions were most similar to those when plant data were collected.

A species list of vascular plants, invertebrates and waterbirds was compiled for each wetland based on scoring all plant species within a variable number of 100 m^2 quadrats at the wetland (Lyons *et al.*, 2004), taking two 50 m invertebrate sweeps (Pinder *et al.*, 2004), and surveying either the whole wetland, or a large section of it, for waterbirds. We use the term "species" loosely to refer to the animal and plant units used in analysis. Identifications were usually at species level but existing taxonomic keys enabled some invertebrate groups to be distinguished only at high taxonomic levels (e.g. Nematoda). Even when keys were adequate, it was sometimes impossible to identify all animals or plants of a genus to species level because specimens were immature or sterile and then it was necessary to lump identifications at genus level for analysis.

Analysis

Singleton species were excluded from the data-set for all multivariate analyses. Wetlands were classified into types according to the similarity of their biota using the PATN analysis package (Belbin, 1993) and presence/absence species data. Czekanowski's coefficient was used as a measure of dissimilarity and under-estimated dissimilarities (>0.95) were re-calculated using the Shortest Path option. The Unweighted Pair-Group Mean Average (UPGMA) fusion method, with β=-0.1, was used to group wetlands (Sneath and Sokal, 1973). The discreteness of wetland types identified by classification was examined by ordination using Semi-Strong Hybrid Multidimensional Scaling (SSH) (Belbin, 1991).

Species were classified into assemblages of species with similar patterns of occurrence using the Two-Step coefficient of dissimilarity (Austin and Belbin, 1982) and UPGMA. The degree of nestedness in each assemblage was calculated using NESTED (Atmar and Patterson, 1993, 1995). Nestedness was further examined by checking that richness of each assemblage was unimodally distributed against 1-dimensional ordination scores of community structure, derived by SSH without masking singletons. Whether richness values of each assemblage fitted a Poisson distribution was checked by visual inspection after plotting them.

For each assemblage that appeared to be ecologically meaningful, the relationship between species richness of the assemblage and environmental attributes across the 197 wetlands was modelled using a generalised linear model (Poisson regression) in the STATISTICA analysis package (StatSoft, 2001). The environmental attributes available for modelling related to geography, climate, water physico-chemistry and two particular habitats (Table 1). Environmental

Table 1 Environmental attributes measured at, or derived for, each wetland and used in modelling. Ionic ratios calculated using milliequivalent values.

Code	Attribute	Code	Attribute
Geographic		Turb	Turbidity (NTU)
Lat	Latitude (°S)	Col	Colour (TCU)
Long	Longitude (°E)	Sil	Silica (mg L^{-1})
Alt	Altitude (m)	Na^+	Sodium (% meq)
Climatic		Ca^{2+}	Calcium (% meq)
Tann	Annual average temperature (°C)	Mg^{2+}	Magnesium (% meq)
Pann	Annual average precipitation (mm)	K^+	Potassium (% meq)
Pdry	Driest quarter precipitation (mm)	Mn^{2+}	Manganese (% meq)
Pcv	Coefficient of variation precipitation	Cl^-	Chloride (% meq)
Evap	Annual average pan evaporation (mm)	HCO_3^-	Bicarbonate (% meq)
Physico-chemical		SO_4^{2-}	Sulphate (% meq)
Sal[1]	Total dissolved solids (mg L^{-1})	DMC	$Mg^{2+} + Ca^{2+} : Cl^-$
pH[1]		CS	$Ca^{2+} : SO_4^{2-}$
Alk	Mg L^{-1} calcium carbonate	CC	$Ca^{2+} : HCO_3^- + CO_3^{2-}$
TN	Dissolved persulphate nitrogen (mg L^{-1})	**Habitat**	
TP	Dissolved persulphate phosphorus (mg L^{-1})	Rock	Waterbody on granite outcrop
Chl	Chlorophyll *a,b,c*, Phaeophytin (mg L^{-1})	Flow	Flowing water when sampled

[1] Used as either a continuous or categorical variable

attributes were screened before constructing each model and attributes that were not significantly related to richness of the assemblage were excluded from the regression analysis. If several attributes were strongly inter-correlated, only the one with most obvious biological meaning was included in analysis. A regression equation was constructed with two to four environmental attributes, using the Best Subsets routine. Significance of the equation was assessed using the Wald statistic after checking that outliers were not disproportionately influencing coefficients. The amount of variation explained was calculated by an R^2-value adjusted for number of cases and environmental variables used (Tabachnik and Fiddell, 1983).

In an attempt to define the habitat preferences of different assemblages, their fidelity to each wetland type was calculated as:

$$F_{Ai} = p_{Ai} \cdot \bar{w}/w_i \cdot \frac{(1/\Sigma p_{Ai} \cdot \bar{w}/w_i)}{1\text{-}n}$$

where F_{Ai} is the fidelity of assemblage A to wetland type *i*, p_{Ai} is the proportion of assemblage A in wetland type *i*, w_i is the number of wetlands in type *i* and w^- is the average number of wetlands per type (see Boesch, 1977).

The WBS results were used to identify some Potential Recovery Wetlands (PRWs) that could form the core of future BRCs. The PRWs represent the surveyed wetlands containing the largest proportion(s) of the assemblages that appeared to need active protection to persist in the surveyed area in the face of further salinisation. The proportion of each assemblage that would be conserved if the PRWs and existing BRCs were protected while the remainder of the surveyed area became salinised was calculated to provide notional indication of the adequacy of the proposed PRWs. The calculation assumed eventual loss of all species outside the PRWs and BRCs, although we recognize the assumption is unrealistic (see Halse *et al*., 2003).

RESULTS

Altogether, 986 wetland or wetland-associated plant, 844 aquatic invertebrate and 57 waterbird species were recorded, with an average of 73 (range 10–174) species per wetland (Appendix 2). Fifteen per cent of plant species were naturalised aliens (weeds). Species occurrence was very patchy with 34% of species occurring at a single wetland, 15% at two wetlands and only 1.1% at more than one-third of sites. No species was present at all wetlands and five of the 10 more common 'species' were higher level taxa. The more common true species were the chironomid midge *Procladius paludicola* (58% of wetlands), introduced herbs *Hypochaeris glabra* (54%) and *Sonchus oleraceus* (43%), introduced grass *Parapholis incurva* (49%) and grey teal *Anas gibberifrons* (48%).

Species assemblages

After deleting singleton species from the data-set, 22 species assemblages were recognized but three of these appeared to be artefacts driven by the species array at individual sites (assemblage 15 by Lake Pleasant View SPM024, 19 by Arro Swamp SPS183, 22 by Goonaping Swamp SPS023) (Appendix 3). Information about assemblages is summarized in Table 2. The assemblages were:

Assemblage 1. A group of 27 species mostly

Table 2 Fidelity matrix of species assemblages (rows) to wetland types (columns). N represents the number of wetlands of each type or the number of times an assemblage member was recorded, $\bar{S}$ and S represent the mean (±SE) number of species per wetland and the number of species in each assemblage, respectively. Mean TDS (g L^{-1}) at wetlands of each type and for occurrences of members of each assemblage, and mean pH at wetlands of each type are also shown. See text for method of calculating fidelity.

	Wetland type																		
	VII	I	VIII	IX	II	VI	IV	V	III	XI	X	XII	XV	XVI	XIII	XIV			
N	13	13	5	12	18	11	12	12	10	4	25	11	22	8	12	9			
$\bar{S}$	88±6	100±9	69±13	108±5	78±3	74±5	88±5	68±7	103±4	73±6	54±3	59±5	73±4	23±5	52±6	50±6			
TDS	0.4±0.2	0.5±0.1	0.5±0.2	1.1±0.4	4.0±0.9	3.8±1.0	4.3±0.6	4.5±1.1	5.8±1.1	16±3	39±6	48±16	51±8	116±27	128±21	146±35			
pH	7.2±0.2	8.0±0.1	7.6±0.4	7.0±0.2	8.0±0.2	7.6±0.2	8.5±0.2	8.4±0.2	8.2±0.2	7.6±0.3	8.8±0.2	8.6±0.2	8.9±0.2	4.7±0.7	8.0±0.1	5.1±0.7	S	N	TDS
Assemblage																			
21	0.796	0.006	0.102	0.000	0.036	0.007	0.024	0.018	0.007	0.000	0.000	0.000	0.003	0.000	0.000	0.000	53	169	0.6±0.3
20	0.307	0.171	0.237	0.081	0.066	0.029	0.009	0.020	0.050	0.005	0.000	0.012	0.010	0.000	0.002	0.002	74	516	2.2±0.6
1	0.007	0.561	0.221	0.014	0.033	0.015	0.035	0.014	0.025	0.042	0.021	0.000	0.000	0.011	0.000	0.000	27	127	2.6±1.0
17	0.054	0.058	0.082	0.404	0.016	0.093	0.104	0.078	0.059	0.023	0.010	0.012	0.003	0.002	0.001	0.001	89	854	3.0±0.4
18	0.055	0.007	0.000	0.808	0.003	0.013	0.028	0.008	0.019	0.048	0.000	0.000	0.002	0.000	0.004	0.005	84	244	3.3±1.3
16	0.221	0.088	0.183	0.266	0.025	0.021	0.019	0.030	0.018	0.068	0.011	0.037	0.004	0.000	0.008	0.000	51	232	4.3±1.1
5	0.081	0.149	0.076	0.069	0.110	0.079	0.095	0.096	0.133	0.036	0.044	0.009	0.012	0.001	0.004	0.006	64	2381	4.9±0.3
4	0.051	0.051	0.024	0.212	0.010	0.434	0.146	0.035	0.006	0.000	0.005	0.000	0.005	0.008	0.005	0.007	62	191	7.1±2.5
8	0.069	0.103	0.051	0.082	0.036	0.128	0.168	0.124	0.135	0.142	0.046	0.021	0.002	0.010	0.007	0.008	70	889	7.2±0.7
2	0.027	0.088	0.025	0.002	0.097	0.193	0.132	0.134	0.144	0.026	0.061	0.013	0.023	0.010	0.021	0.005	106	577	11±1
3	0.011	0.007	0.029	0.036	0.011	0.082	0.127	0.020	0.048	0.334	0.023	0.199	0.000	0.006	0.036	0.032	61	183	24±3
6	0.039	0.077	0.025	0.033	0.069	0.059	0.093	0.073	0.110	0.067	0.156	0.059	0.056	0.025	0.033	0.027	35	2124	24±1
7*	0.119	0.142	0.049	0.045	0.107	0.032	0.027	0.016	0.079	0.061	0.068	0.044	0.061	0.017	0.095	0.036	31	452	26±2
9	0.008	0.007	0.022	0.065	0.019	0.028	0.152	0.022	0.078	0.271	0.060	0.180	0.017	0.019	0.043	0.010	30	439	26±2
12	0.126	0.043	0.154	0.004	0.233	0.037	0.009	0.009	0.056	0.000	0.021	0.019	0.179	0.006	0.013	0.091	63	270	32±4
13	0.018	0.030	0.010	0.004	0.056	0.012	0.028	0.031	0.090	0.050	0.263	0.087	0.117	0.039	0.074	0.090	68	2236	44±1
14	0.022	0.004	0.019	0.000	0.109	0.000	0.003	0.006	0.048	0.005	0.085	0.036	0.353	0.029	0.093	0.188	37	802	59±2
11	0.000	0.000	0.000	0.000	0.052	0.000	0.000	0.010	0.023	0.000	0.038	0.011	0.629	0.015	0.107	0.116	44	156	64±4
10	0.002	0.003	0.012	0.000	0.030	0.000	0.007	0.005	0.002	0.005	0.120	0.125	0.100	0.085	0.302	0.204	100	603	90±3

Figure 4 Distribution of species assemblages at wetlands surveyed in the wheatbelt. Assemblages 1–6.

associated with fresh water (mean 2.6±1.0 g L^{-1}) that represented 0.9% of species occurrences in the survey. The assemblage contained 11 invertebrate, 1 waterbird and 15 plant species. Members were absent from most wetlands and the assemblage tended to occur in the eastern central and southern wheatbelt (Figure 4). It was best represented at Lake Cronin (SPS003, 15 species).

Assemblage 2. A group of 106 species found mostly in association with subsaline water (mean 10.6±1.1 g L^{-1}). The assemblage contained 54 invertebrate, 10 waterbird and 42 plant species and represented 4.3% of all species occurrences. Members of the assemblage were distributed throughout the wheatbelt, with few at any one site (Figure 4). The assemblage was best represented at Murchison River (SPS198, 29 species).

Assemblage 3. A group of 61 species found mostly in or adjacent to saline rivers and wetlands of the south coast (mean 23.5±1.1 g L^{-1}) (Figure 4). The assemblage contained 29 invertebrate, 1 waterbird and 31 plant species and represented 1.4% of all species occurrences. The assemblage was best represented at the Oldfield River (SPS123, 12 species).

Assemblage 4. A group of 62 species in or associated with fresh to subsaline, flowing water (mean 7.1±2.5 g L^{-1}). The assemblage contained 38 invertebrate and 24 plant species and represented 1.4% of all species occurrences. Members were concentrated at stream sites in wandoo woodland east of Perth (Figure 4) and the assemblage was best represented at Jimperding Brook (SPS004, 20 species).

Assemblage 5. A group of 64 species widely distributed in the wheatbelt (Figure 4) in association with fresh to subsaline water (mean 4.9±0.3 g L^{-1}). The assemblage contained 56 invertebrate, 1 waterbird and 7 plant species, representing 17.7% of all species occurrences, and was best represented at Range Road yate swamp (SPS033, 39 species).

Assemblage 6. A group of 35 widespread (Figure 4), salt-tolerant species (mean 23.7±0.9 g L^{-1}). The assemblage contained 12 invertebrate, 10 waterbird and 13 plant species, representing 15.8% of all species occurrences, and was best represented at Dulbinning Lake (SPS007, 25 species).

Assemblage 7. A group of 31 species found over the full range of salinities (mean 26.1±2.3 g L^{-1}) (Table 2). The assemblage, which contained 10 invertebrate, 1 waterbird and 20 plant species, was patchily distributed across the whole wheatbelt and represented 3.4% of all species occurrences. Plant species were nearly all exotic weeds, without conservation value. The assemblage was best represented at Arro Swamp (SPS183, 14 species).

Assemblage 8. A group of 70 species found mostly in fresh to subsaline or weakly saline water (mean 7.2±0.7 g L^{-1}). The assemblage contained 47 invertebrate, 2 waterbird and 21 plant species, representing 6.6% of all species occurrences. It was patchily distributed throughout the wheatbelt but with a tendency for greater frequency of occurrence on the south coast (Figure 5). It was best represented at Boyacup Bridge swamp (SPS111, 20 species).

Assemblage 9. A group of 30 halobiont species (mean 26.1±2.0 g L^{-1}) that occurred most frequently along the south coast and south-western part of the study area (Figure 5). The assemblage contained 11 invertebrate, 1 waterbird and 18 plant species, representing 3.3% of all species occurrences. It was best represented at Oldfield River (SPS123, 15 species).

Assemblage 10. A group of 100 species associated with saline and hypersaline water (mean 90±3 g L^{-1}) outside high rainfall and, usually, coastal areas (Figure 5). The assemblage was dominated by plants, containing 22 invertebrate, 7 waterbird and 71 plant species, which represented 4.9% of all species occurrences. The site with most species of the assemblage was Isthmus Lake (SPS058, 24 species).

Assemblage 11. A group of 44 species associated with hypersaline water (mean 64±4 g L^{-1}) of the north-eastern wheatbelt (Figure 5). The assemblage comprised almost exclusively plants with 2 invertebrate, 1 waterbird and 41 plant species, which represented 1.2% of all species occurrences. It was best represented at Lake Moore (SPS148, 19 species).

Assemblage 12. A group of 63 species associated with some of the freshest and some of the most hypersaline wetlands (mean 31.8±3.6 g L^{-1}) in the north-eastern wheatbelt (Figure 5). The assemblage was dominated by 47 plants species which, together with 16 invertebrate species, represented 2.0% of all species occurrences. There was considerable discrepancy between plants and invertebrates in terms of the salinities with which they were associated (Table 3). The assemblage was best represented at Yarra Yarra Lake (SPS162, 12 species).

Assemblage 13. A group of 68 species most commonly found in or near secondarily saline wetlands (mean 44±1 g L^{-1}). The assemblage was widespread in the wheatbelt (Figure 5) and accounted for 16.6% of all species occurrences. It comprised 27 invertebrate, 4 waterbird and 37 plant species and was best represented at Lakes

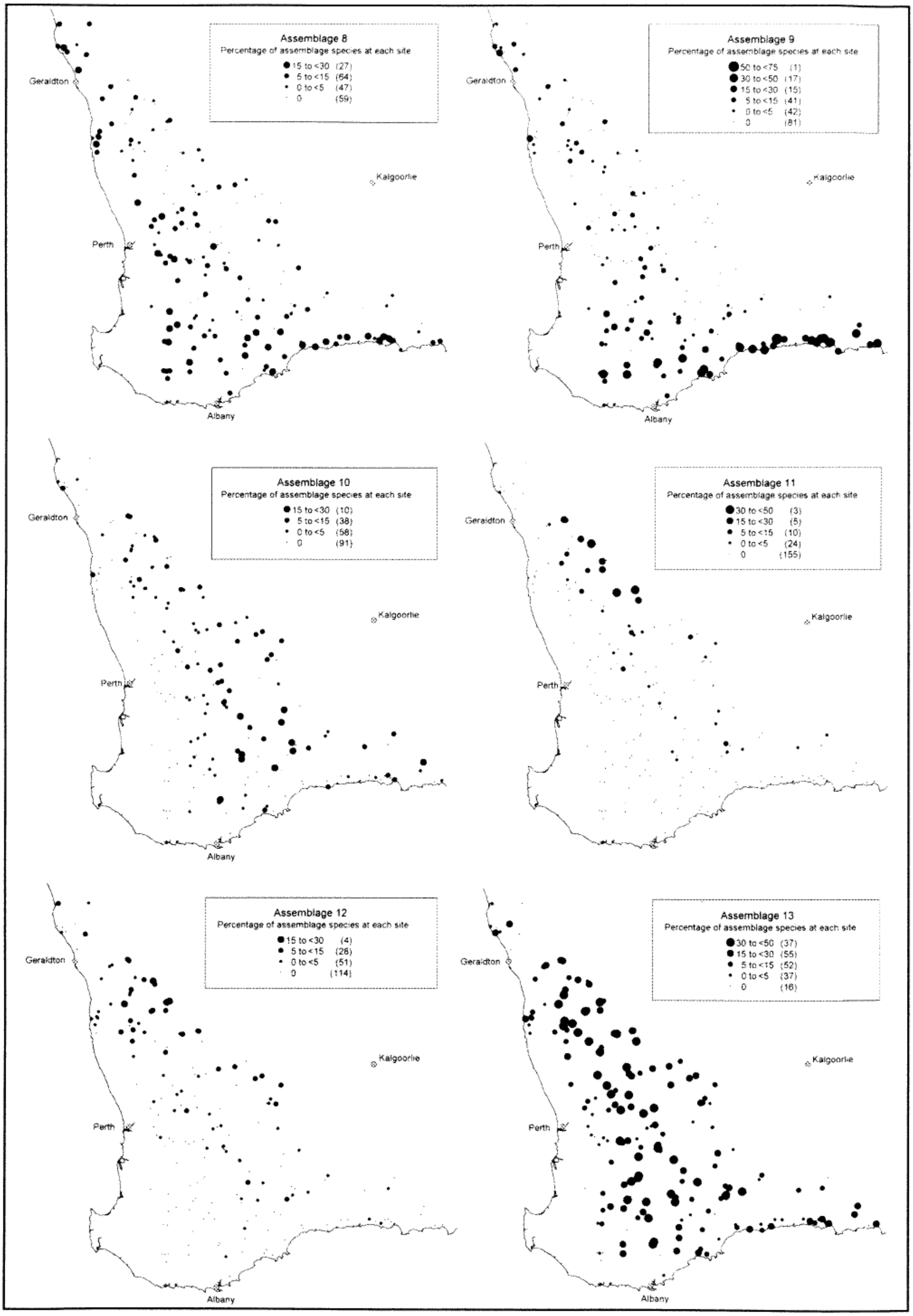

Figure 5 Distribution of species assemblages at wetlands surveyed in the wheatbelt. Assemblages 8–13.

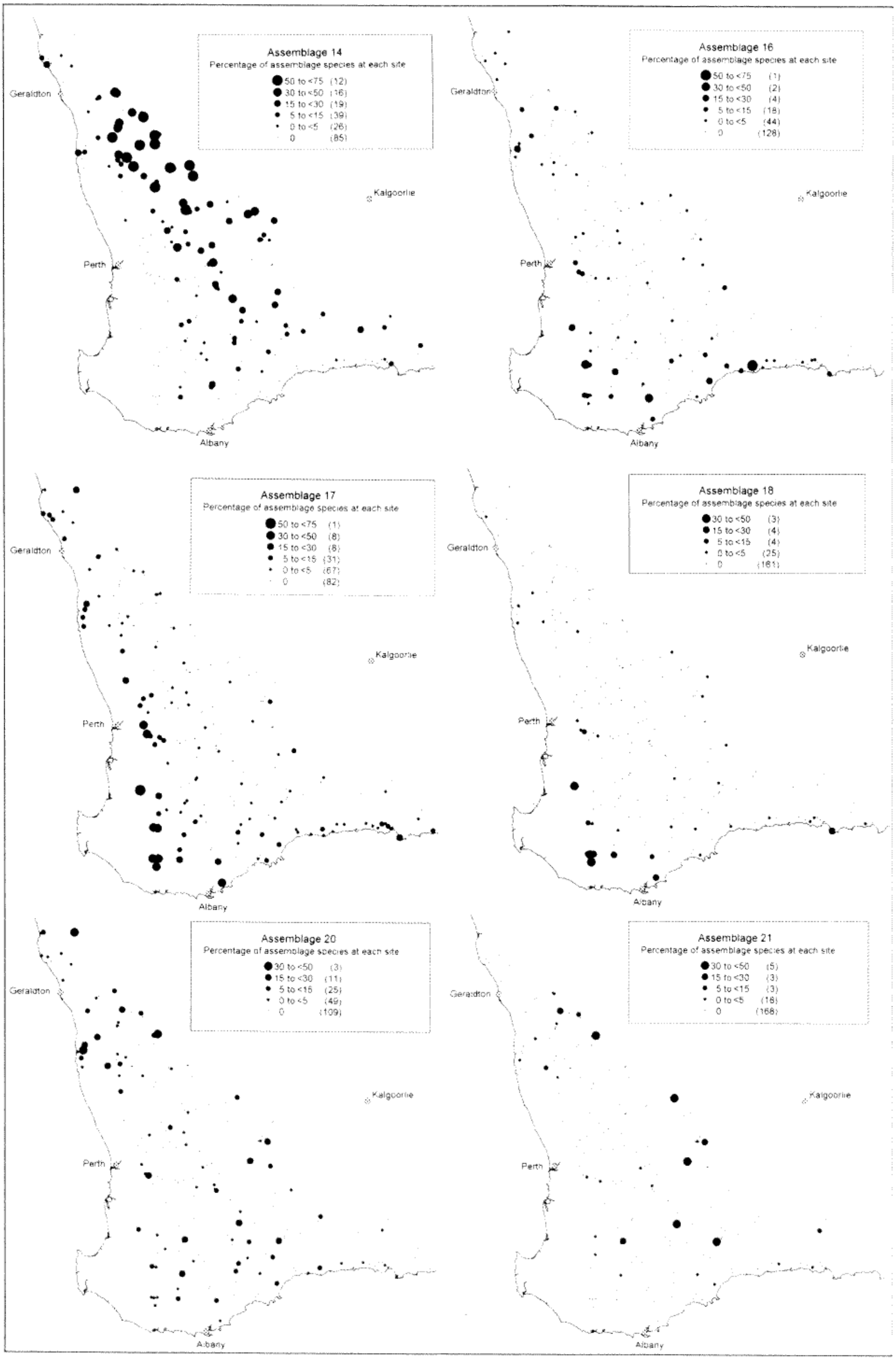

Figure 6 Distribution of species assemblages at wetlands surveyed in the wheatbelt. Assemblages 14–21.

Table 3 Mean (±SE) salinity of occurrence (g L^{-1}) of plant, invertebrate and waterbird species in each assemblage. SE shown only if there were ≥5 occurrences in a category

Assemblage	Plants	Invertebrates	Birds
21	0.9±0.7	0.4±0.1	–
20	3.7±1.6	1.3±0.2	–
1	3.2±1.6	1.0±0.2	–
17	4.3±0.8	2.3±0.4	1.4±0.5
18	4.1±2.2	2.4±0.9	–
16	7.6±2.3	1.8±0.6	–
5	12.2±2.3	4.2±0.2	6.7±2.1
4	14.6±6.7	2.7±0.5	–
8	11.8±2.0	5.1±0.6	10.7±3.0
2	20.3±3.1	5.6±0.5	5.6±0.7
3	25.3±4.8	21.6±3.2	22.0
6	32.1±1.9	20.6±1.3	15.8±1.2
7	30.4±3.1	14.5±2.5	23.8±16.6
9	28.6±2.8	22.6±2.9	12.2±5.1
12	38.1±4.3	10.7±5.1	–
13	50.3±1.8	34.1±1.4	43.1±4.5
14	58.4±2.2	–	68.0±12.6
11	62.5±4.3	67.0	108.0±24.1
10	88.7±3.9	91.9±5.7	84.9±9.8

Biddy and Coyrecup (SPS067 and SPM004, 33 species).

Assemblage 14. A group of 37 species typical of naturally hypersaline wetlands (mean 59±2 g L^{-1}) in the northern wheatbelt, although more widely distributed (Figure 6). The assemblage comprised almost exclusively plants (36 species) which, together with 1 waterbird species, represented 6% of all species occurrences. The assemblage was best represented at Weelhamby Lake and Mongers samphire pan (SPS169 and SPS167, 25 species).

Assemblage 16. A group of 51 species occurring predominantly around fresh water although mean salinity was 4.3±1.1 g L^{-1} because of isolated plant occurrences around hypersaline wetlands. The assemblage was more common in high rainfall areas and the south coast (Figure 6). It consisted of 30 invertebrate and 21 plant species, representing 1.7% of all species occurrences and was best represented at Youlabup Swamp (SPS124, 26 species).

Assemblage 17. A group of 89 species associated with fresh to subsaline water (mean 3.0±0.4 g L^{-1}) predominantly on the western margin of the wheatbelt (Figure 6). The assemblage contained 54 invertebrate, 1 waterbird and 34 plant species, representing 6.4% of all species occurrences. It was best represented at Nalyerin Lake (SPS031, 49 species).

Assemblage 18. A group of 84 species almost completely restricted to sedge swamps, with greatest occurrence in swamps of the south-western part of the study area (Figure 6). While the majority of occurrences were in fresh water, mean salinity of occurrence was 3.3±1.3 g L^{-1} as a result of a few plant records around hypersaline wetlands. The assemblage contained 35 invertebrate and 49 plant species, representing 1.8% of all species occurrences. It was best represented at Poorginup Swamp (SPS103, 39 species).

Assemblage 20. A group of 74 species patchily distributed though the wheatbelt (Figure 6) and occurring predominantly in fresh water (mean 2.2±0.6 g L^{-1}). The assemblage contained 41 invertebrate, 1 waterbird and 32 plant species, representing 3.8% of all species occurrences. It was best represented at Punjerwerry Claypan and Weelawadji Lake (SPS197 and 177, 34 species).

Assemblage 21. A group of 53 species typical of pools on granite outcrops (mean 0.6±0.3 g L^{-1}, Figure 6). The assemblage contained 27 invertebrate and 26 plant species, representing 1.3% of all species occurrences. It was best represented at Wannara Rock (SPS168, 21 species).

Several trends were noticeable among assemblages. Firstly, waterbirds rarely formed a significant component of the species richness of an assemblage: even in the most bird-dominated assemblage 6, waterbirds comprised only 29% of taxa. Plants comprised most of the biota of naturally saline assemblages. The ratio of plants: plants+invertebrates averaged >0.9 in the assemblages most typical of naturally hypersaline sites (10, 11 and 14) compared with <0.5 in other assemblages

Secondly, many assemblages occurred at all wetland types, albeit often at very low frequency (Table 2). This was largely attributable to many plant species that grew on dunes or rises around a wetland not closely reflecting conditions in the waterbody itself and being widely distributed across wetland types. For most assemblages, the average wetland salinity associated with plant records was higher than for invertebrate records. The discrepancy increased as the assemblage became more halophilic, except for assemblages occurring predominantly at hypersaline wetlands (Table 3).

Thirdly, few assemblages were tightly defined spatially and the occurrence of assemblages was often patchy. For example, wetlands containing significant numbers of assemblage 4 species were located near Geraldton, Perth and Esperance with only scattered, low-frequency occurrence at wetlands between (Figure 4). The somewhat stochastic occurrence of assemblages was reflected in the relatively low number of assemblage species at individual sites. Even the site best representing an assemblage contained, on average, only 45% of assemblage species (range 20–71%).

Table 4 Equations predicting the logarithm of species richness (S) at each site for each species assemblage and the degree of nestedness of assemblages. The adjusted R^2 is a measure of how much variation in assemblage richness is explained by each equation; *T* and *% fill* are measures of noise and the frequency of occurrence of species in the assemblage, and *P* is the probability that an assemblage is not nested (Atmar and Patterson 1995). See Table 1 for abbreviations and footnote for categories of salinity[1] and pH[2].

Assemblage	Equation for Log_e S	*Adj* R^2	*T*	*% fill*	*P*
1	2.3644 - 0.0457 Pcv + 0.0405 HCO_3 - 0.1034 SO_4 - 0.0374 Sal[1]	62	16	11	$1e^{-5}$
2	-12.4464 - 0.0176 Sal + 0.0024 Alk + 0.0285 Pcv + 0.0995 Long	33	8	4	$4e^{-22}$
3	-11.7119 + 1.3273 flow + 0.3931 latitude - 0.0068 elevation - 0.1572 Ca:SO_4 meq	53	11.3	5	$2e^{-1}$
4	-4.8503 + 1.3979 Flow + 0.0050 Pann + 0.0184 Pcv + 0.0495 Mg	47	11	6	$3e^{-3}$
5	7.3355 - 0.0532 Sal - 0.0362 Long	70	33	23	$8e^{-95}$
6	2.6369 - 0.0040 Sal - 0.7251 pH1 - 0.1397 pH2 - 10.8641 Mn	33	38	31	$2e^{-78}$
8	-.0358 + 1.0679 Sal1 + 1.5586 Sal2 + 0.6770 Sal3 + 0.0367 Mg - 0.0405 CC	55	22	9	$3e^{-28}$
9	-9.6860 + 0.3569 Lat – 0.0062 Alt – 1.9000 Sal1 – 0.0681 Sal2 + 0.4372 Sal3	59	22	12	$5e^{-17}$
10	3.0831 – 0.0180Pcv –3.2756 Sal1 – 2.8694 Sal2 – 0.6227 Sal3	57	10	6	$3e^{-35}$
11	-5.3949 + 0.6050 Tann -0.0235 Pann - 10.6212 Sal1 - 2.8034 Sal2 - 0.6572 Sal3 + 0.3606 pH	75	16	8	$2e^{-4}$
12	- 3.8148 + 0.0108 Alt - 0.0658 Mg - 0.0030 Sal - 0.0026 Pann	51	12	5	$2e^{-4}$
13	3.6323 – 0.0020 Pann – 1.2524 Sal1 – 0.8087 Sal2 + 0.2018 Sal3 – 0.7926 pH1 – 0.2944 pH2	53	26	18	$2e^{-97}$
14	- 2.4369 + 0.0093 Evap – 2.4704 Sal1 – 1.4907 Sal2 – 0.0581 Mg	65	23	19	$2e^{-49}$
16	-9.8974 + 0.4045 Lat – 0.0383 Sal – 0.3998 pH + 0.1901 K	43	13	6	$5e^{-8}$
17	-10.2881 + 0.2703 Lat + 0.0038 Pann + 0.0268 Pcv – 0.0709 Sal	76	9	8	$2e^{-71}$
18	-14.5642 + 3.9927 logPann - 0.6591 Tann + 1.3916 pH2 - 0.0005 TN	84	13	8	$2e^{-10}$
20	3.7039 + 0.6485 Rock – 0.0930 Sal – 0.0044 Alk – 0.0254 Cl	63[3]	12	8	$4e^{-36}$
21	-2.7073 + 2.9708 Rock + 0.1348 SO_4 – 0.8150 CC	86	15	11	$6e^{-9}$

[1] Sal1 < 150 mg L^{-1}, Sal2 < 8000 mg L^{-1}, Sal3 < 50 000 mg L^{-1}, Sal4 ≥ 50 000 mg L^{-1}

[2] pH1 < 6.0, pH2 ≥ 6.0

[3] drop SPS025, SPS177 R^2 = 70%

Modelling assemblage occurrence

Species richness values of all modelled assemblages were unimodally distributed across ordination scores, suggesting the assemblages were nested (see also *P*-values in Table 4). Richness values approximated Poisson distributions for all assemblages other than 5 and 13. Equations describing the distribution of species richness were produced for 18 assemblages (no satisfactory model could be constructed for assemblage 7 and no attempt was made to model the artefactual assemblages 15, 19 and 22). Adjusted R^2-values of the equations varied from 33–86% (Table 4).

The low amount of variation (33%) explained by equations for assemblages 2 and 6 appeared to reflect biological reality rather than violation of model assumptions. Both assemblages contained freshwater species that were salt-tolerant and found throughout the wheatbelt (Figure 4) and beyond, so that the WBS did not circumscribe their ecological limits efficiently. A quarter of the species belonging to assemblage 6 were mobile waterbirds, half the invertebrates were higher taxa (usually families or phyla) and many of the plants were weeds. More than half the invertebrates in assemblage 2 had poor dispersal ability and their occurrence may be determined largely by historical events (see Maly *et al.*, 1997 for a discussion of copepod distributions) that are stochastic with regard to the environmental parameters measured in the WBS.

The variables used in models of species richness do not necessarily reflect the main environmental drivers of species distributions or assemblage richness, even when R^2-values are high. However, salinity was an explanatory variable for 14 assemblages (Table 4) and for other assemblages there were significant correlations between salinity and one of the variables used in the model. This strongly suggests salinity is a major driver of community patterns. Other variables that appeared commonly in models were annual rainfall, pH, latitude, alkalinity and magnesium ion concentration, while the presence of a granite outcrop was a strong predictor of the occurrence of assemblage 21 and flowing water was a predictor of assemblages 3 and 4.

Types of wetland

Sixteen types of wetland were recognized in the surveyed area, based on their plant and animal assemblages. The major split in the classification related to the separation of primarily and secondarily saline sites from fresh or subsaline ones (Figure 7, Appendix 4). The major wetland types were:

Type I. Minimally disturbed freshwater swamps. Fresh water (mean 0.5±0.1 g L^{-1}) with either emergent trees, shrubs or grasses on the lake-bed. Supported a high number of ubiquitous species. Mean richness was 95±8, with Arro Swamp (SPS183, 151 species) and Weelawadji Lake (SPS177, 135 species) having the most species-rich communities. Assemblage 1 occurred predominantly in this wetland type (Table 2) and invertebrates (61% of species) dominated the biota.

Type II. Disturbed northern swamps. Fresh to subsaline water (mean 4.0±0.9 g L^{-1}). All member wetlands were in the northern wheatbelt and were disturbed to some extent; most contained emergent vegetation. Mean richness was 76±3, with Tardun CBC swamp (SPS187, 103 species) being the richest. Type II wetlands were significant habitat (>20% of records, adjusted for group size) for species in assemblage 12 and invertebrates (55% of species) dominated the biota.

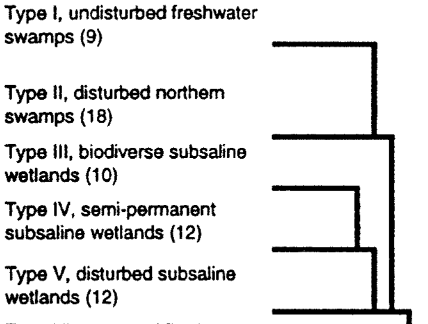

Figure 7 UPGMA classification of wetlands into types based on their biota. Number of wetlands in each type shown.

Type III. Biodiverse subsaline wetlands. Fresh to subsaline water (mean 5.8±1.1 g L^{-1}). Wetlands in this group had little in common with each other. Lake Logue (SPM002) on the coast south of Geraldton was in the final stages of drying and had become saline as it evapo-concentrated, the secondarily saline Lake Dulbinning (SPS007) in the central wheatbelt filled a month or so prior to sampling and was fresher than usual, Capamouro Swamp (SPS163) in the northern wheatbelt usually contains hypersaline water (if water present) but was subsaline when sampled because of a large flood event, and Peenebup Creek (SPS115) is a subsaline river flowing towards the south coast. Mean richness was 100±3, with Boyacup Bridge swamp (SPS111, 113 species) the richest site. Most of the assemblages found at wetlands of intermediate salinities occurred at low frequency in type III wetlands; invertebrates formed a greater percentage of the biota (52% of species) than plants (39%).

Type IV. Semi-permanent subsaline wetlands. Fresh to subsaline water (mean 4.3±0.6 g L^{-1}). Mostly on south coast, usually with extensive fringing trees. Mean richness was 84±5, which was almost 20% lower than type III. The assemblages occurring in the two wetland types were similar, with type IV wetlands differentiated largely by a greater proportion of species in assemblages 3 and 9. Invertebrates dominated the biota (57% of species) but more waterbird species were present (13%) than at any other wetland type except X. The richest site was Meeking Lake (SPS038, 102 species).

Type V. Disturbed subsaline wetlands. Fresh to subsaline water (mean 3.6±0.7 g L^{-1}, excluding SPS199 where sampling included areas much fresher than the recorded salinity). Occurred throughout the wheatbelt, other than the south coast. Mean richness was 67±6, which was more than 30% lower than type III and the number of assemblages making use of the wetlands was fewer than for III and IV (Table 2). Invertebrates were very much the dominant element of the biota (71% of species) with the lower species richness in type V wetlands largely the consequence of a depauperate flora. The richest site was Qualeup Lake (SPS032, 126 species), which had almost twice as many species as any other wetland in the group.

Type VI. Westward flowing rivers. Fresh to subsaline water (mean 3.8±1.0 g L^{-1}). Mean richness was 70±4, with Skelton Gully (SPS193, 97 species) being the most species-rich site. Half the records of assemblage 4 occurred in this wetland type and several other assemblages of intermediate salinities also occurred at moderate frequency; invertebrates dominated the biota (70% of species).

Type VII. Granite rock pools and vernal pools. With their very small, mostly hard rock, catchments these sites were the least saline of any wetland type (mean 0.4±0.2 g L^{-1}). There were two obvious sub-groups: pools on granite outcrops and three shallow, clay-based vernal pools plus a shallow creek high in the landscape. Mean richness was 82±5, with Wanarra Rock (SPS176, 117 species) being the most species-rich site. Type VII wetlands were the dominant habitat for assemblage 21, with assemblages 20 and 16 also occurring in significant proportions. Slightly more invertebrate species (55%) were present than plants (45%).

Type VIII. Claypans and shallow yate swamps. Two groups of wetlands occurred within this type: turbid claypans and clear-water shallow yate swamps. Both were fresh (mean 0.5±0.2 g L^{-1}). Mean richness was 62±12, with Punjerwerry Claypan (SPS197, 100 species) being the richest site. Assemblages 20, 1 and 16 occurred in significant proportions; the biota was dominated by invertebrates (70% of species).

Type IX. Sedge swamps. Fresh water (1.1±0.4 g L^{-1}). Mean richness was 98±5, with Nalyerin Lake (SPS031, 130 species) being the richest site. These wetlands provided the main habitat for assemblage 18, and significant habitat for assemblages 17, 16 and 4. The biota was dominated by invertebrates (63% of species).

Type X. Secondarily saline wetlands. Almost all these wetlands contained fresh or subsaline water prior to land clearing but are now more saline (Bennetts Lake SPS077 may be a naturally saline exception). Mean salinity was 38.7±6.5 g L^{-1} and mean richness 54±3, with Stennetts Lake (SPS075, 71 species) the richest site. The wetlands provided significant habitat for assemblage 13 and most assemblages typical of saline water were present at low frequencies. Half the species were plants, with waterbirds comprised 13% of the community to make type X (together with IV) the wetland type supporting most waterbird species.

Type XI. Saline south coast rivers. Three south coast rivers and an adjacent swamp that appeared to cluster with rivers on the basis of plant composition. Saline water (16.0±6.5 g L^{-1}) and mean richness 68±6, with Oldfield River (SPS123, 68 species) the richest of the river sites. The sites appeared to be important habitat for species of assemblages 3 and 9, although small group size means this conclusion should be treated cautiously. Invertebrates comprised the largest proportion of the biota (58% of species).

Type XII. Coastal saline lakes. Saline water (47.9±16.5 g L^{-1}). The two subsaline wetlands in this group (SPS121, SPS122) were saline but freshened after rain shortly before sampling (Pinder *et al.*, 2004a). The wetlands were located on the coastal plain of the south and west coasts and had mean richness 56±4, with Mullet Lake (SPS141, 82 species) the richest site. Assemblages 3 and 9 occurred in type XII wetlands in significant proportions; just over half the biota (53%) comprised plant species.

Type XIII. Alkaline hypersaline playas. Hypersaline (128±21 g L^{-1}), alkaline (8.0±0.1) water. Primarily hypersaline playa lakes, mean richness 50±6, with Anderson Lake (SPS106, 94 species) being the richest site. Assemblage 10 occurred in significant proportions and other assemblages associated with high salinities were present in low frequencies. Plants dominated the biota (76% of species).

Type XIV. Species-rich acidic hypersaline playas. Hypersaline (146±35 g L^{-1}), acidic water (4.6±0.6, excluding the alkaline Kondinin samphire marsh SPS017 which had a salinity of 10 g L^{-1} and pH of 9.2). Primarily hypersaline playa lakes, mean richness 49±6, with Crook's wetland (SPS076, 58 species) being the richest acidic site. Assemblage 10 occurred in significant proportions and other assemblages associated with hypersaline conditions were present in low frequencies. Plants dominated the biota (80% of species).

Type XV. Saline playas. Saline water (51±8 g L^{-1}). Primarily saline and alkaline, mean richness 71±3, with Mongers samphire pan (SPS167, 114 species) being the richest site. Assemblages 11 and 14 occurred in significant proportions and most other assemblages typical of saline conditions were present. Plants dominated the biota (66% of species).

Type XVI. Species-poor acidic hypersaline playas. Hypersaline (116±26 g L^{-1}), acidic water (4.7±0.71, including two sites with pH ~8). Disturbed primarily hypersaline playa lakes, usually with increased inundation as a result of secondary salinisation, these wetlands were depauperate with mean richness 21±4. Wetlands with most species were Masters saline lake SPS097 and Kondinin salt marsh lake (43 and 34 species, respectively) but neither was typical of the type. Only assemblage 10 had more than 5% of its occurrences in this wetland type. Plants dominated the biota (67% of species).

The different wetland groups were comparatively well separated in ordination space (Figure 8), providing evidence that the wetland types identified in Figure 7 represented distinct communities. Sedge swamps and granite rock pools (types IX and VII) were the wetland types in fresh water with most clearly distinguished communities.

The ordination of freshwater wetlands supported a division within type VII between the vernal pools (Goonaping SPS023, Youlabup SPS124 and Ngopitchup SPS102) and granite rock pools, although we did not recognize this in the wetland classification. Claypans and shallow yate swamps (type VIII) formed a heterogeneous group with Punjerwerry Claypan (SPS197) and Frank Hahn National Park claypan (SPS087) having different communities from each other and other type VIII wetlands. Among the saline wetland types, there was considerable heterogeneity within species-poor acidic hypersaline playas (type XVI), which resulted in some overlap with other hypersaline wetlands (types XIII–XV) (Figure 8). Species-rich acidic hypersaline playas and saline playas (types XIV and XV) also showed some overlap with each other. Jurien coastal lake (SPS178) and Hutt Lagoon (SPS189), the only northern wetlands among type XII (predominantly southern coastal saline lakes), were outliers but grouped together.

Singleton species

More than one-third of species were recorded at only one wetland and were excluded from multivariate analyses for mathematical reasons (Belbin, 1993). Plants comprised 55% of all singletons, invertebrates 43% and waterbirds 2%. Within the three elements the percentage singletons was similar for plants and invertebrates (36% and 33%, Figure 9a,b) but lower for waterbirds (19%). Individual wetlands contributed disproportionately to the list of singletons, with 6% of sites accounting for one-quarter of all singletons. Most of these sites were either on the wetter, western side of the wheatbelt or in the north (Figure 10) and it is likely that many of the singletons in these wetlands were species with core ranges outside the wheatbelt, either in the south-west forest or the northern arid zone.

The number of singleton species was significantly correlated with overall species richness at each site ($r = 0.43$) and negatively correlated with salinity ($r = -0.23$) but the relationships had little explanatory power. Most wetland types had few singletons, with sedge swamps (type IX) the most obvious exception (Figure 9c). Individual sites with large numbers of singletons occurred in type I (Arro Swamp SPS183, 23 species), type VI (Murchison River SPS198, 13 species), type VII (Goonaping Swamp SPS023, 24 species) and type IX (Poorginup Swamp SPS103, 22 species). Hypersaline wetlands supported relatively few singletons (Figure 9c), with the greatest number occurring in Kondinin salt marsh lake (SPS016, 7 species). However, the proportion of the flora at individual hypersaline wetlands that were singletons was much higher than for the invertebrate fauna (Figure 9d). Beaumont Nature Reserve (SPS130, 4 species) stood

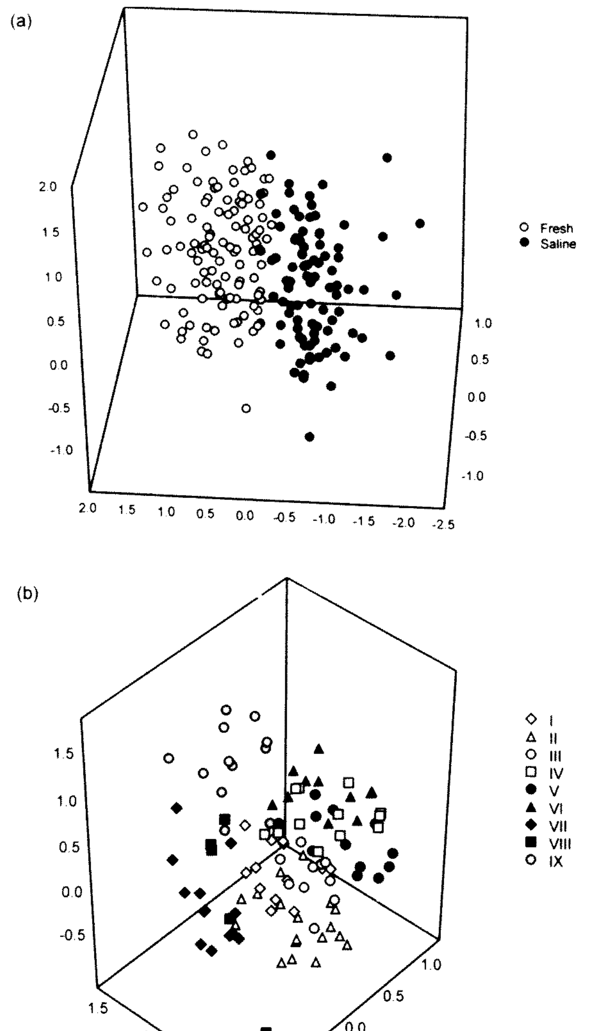

Figure 8 Ordination of wetland groups in the wheatbelt as defined by UPGMA clustering. (a) all groups, (b) freshwater groups I–IX, (c) saline groups X–XVI. Stress = 0.19.

out for its invertebrate singletons. Secondarily saline wetlands (type X) and disturbed subsaline wetlands (type V) supported few singleton species.

DISCUSSION

Waterbird distributions in the wheatbelt and south coast, and the factors controlling them, were well understood prior to the WBS as a result of surveys in the early 1980s (Jaensch *et al.*, 1988; Halse *et al.*, 1993b) but the WBS considerably improved knowledge of invertebrates and vascular plants. For example, it was estimated by Anonymous (1996a) that there were only 200 aquatic invertebrate species in the wheatbelt compared with nearly 1000 now known from the WBS and related monitoring programs (Cale *et al.*, 2004; Pinder *et al.*, 2004). While the vascular flora was better known than aquatic invertebrates, the WBS represented the first systematic floristic survey of wheatbelt wetlands. In particular, knowledge of the naturally saline systems within inland palaeo-channels has been greatly improved. Eight new species were discovered, as well as numerous populations of species previously found in few localities and considered restricted (Lyons *et al.*, 2004). One of the major outcomes of the WBS has been showing that wetland communities of the wheatbelt and south coast are substantially richer and more complex than previously recognized. In addition, the surveyed area has a moderately rich diatom fauna (Blinn *et al.*, 2004). Protection of these biological communities should be a conservation priority.

In terms of localised biodiversity patterns, nearly all wetlands in the Wheatbelt are significant. Average instantaneous numbers of plant, invertebrate and waterbird species associated with wetlands in types I (freshwater), III (biodiverse subsaline) and IX (sedge) were ≥ 100. Only type XVI wetlands (species-poor acidic hypersaline)

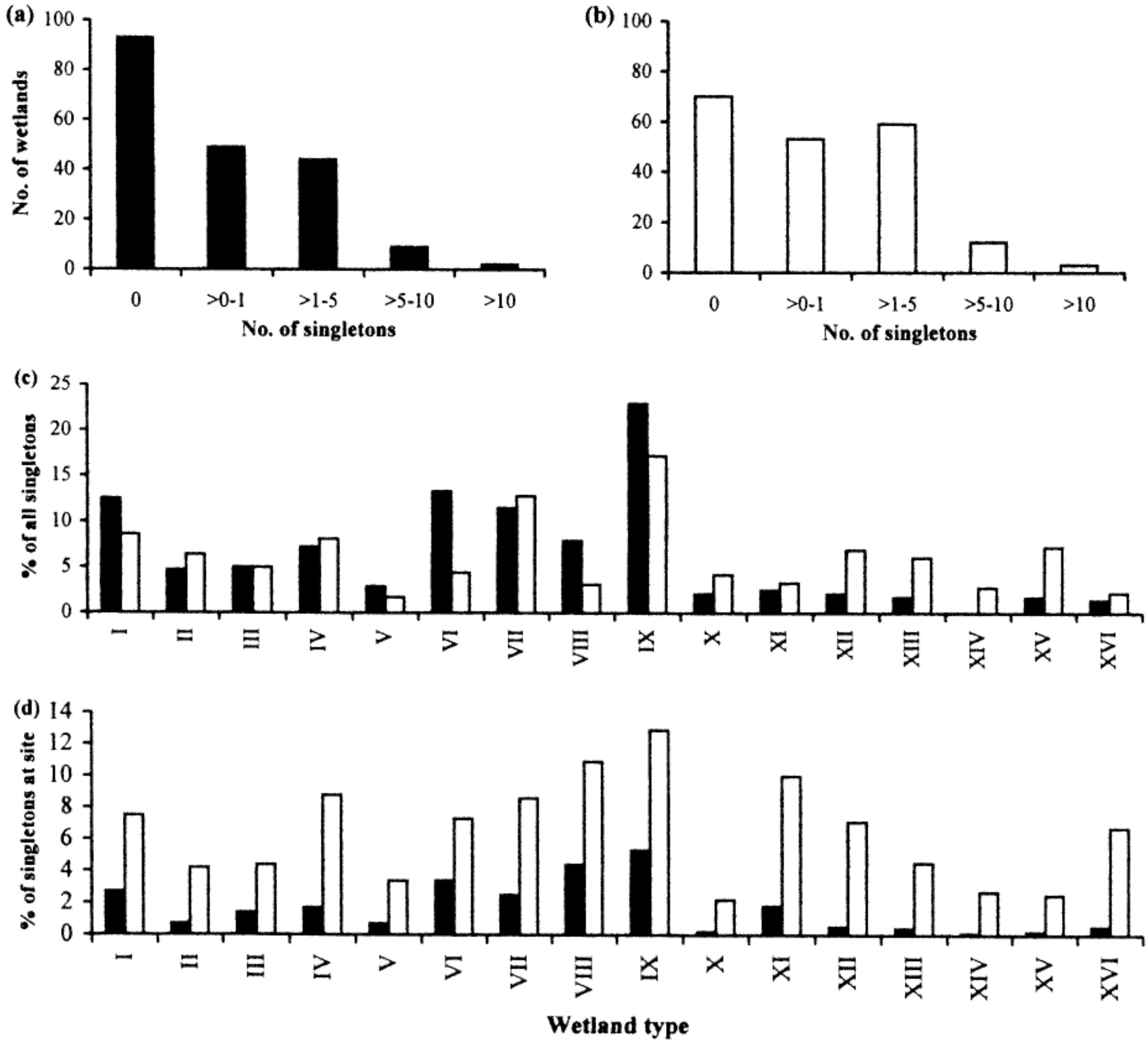

Figure 9 Frequency of occurrence of singletons in wetlands. (a) invertebrates, (b) plants, (c) percentage of all plant or invertebrate singletons in each wetland type, (d) average percentage singletons in the plant or invertebrate species list at wetlands of each type. Invertebrates, solid bars; plants open bars.

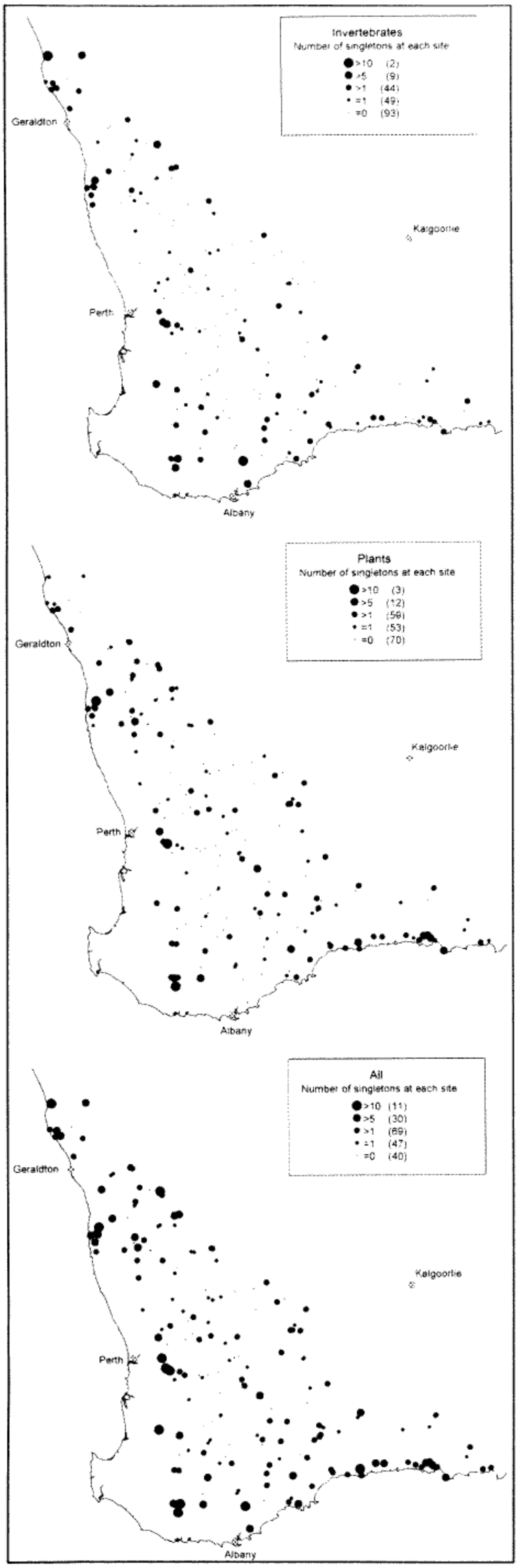

Figure 10 Distribution of singleton species at wetlands surveyed in the wheatbelt.

were depauperate (average of 23 species). However, some wetland types (e.g. X secondarily saline) were dominated by widespread species and their irreplaceability at a regional scale is low (see Pressey *et al.*, 1994). Protection of individual wetlands containing widespread species is usually not critical to maintaining the regional species pool but may be very important for maintenance of the overall populations of some waterbird species (Halse *et al.*, 1995 and references therein).

The most commonly occurring assemblages were 5 (widespread, fresh to subsaline), 8 (fresh to weakly saline, mostly south coast) and 13 (secondarily saline), which accounted for about half the species records (Table 2). The abundance of two salt-tolerant freshwater assemblages reflects the greater richness of the freshwater biota, compared with that of highly saline systems, and the importance of salt tolerance if species are to occur commonly. It should be emphasized, however, that the relative frequency of different assemblages, as perceived by survey analysis, was partly a reflection of sampling design. An attempt was made to sample the full range of natural wetland types in the surveyed area (see Lyons *et al.*, 2004; Pinder *et al.*, 2004) but not necessarily in proportion to their abundance. For example, assemblage 21 (granite specialists) comprised 1% of species records. The assemblage was more-or-less restricted to granite outcrop pools, which represented 5% of the wetlands sampled. Its frequency of occurrence would have increased if more granite pools had been sampled.

Biodiversity patterns and surrogate taxa

Many approaches to reservation, based on mapping plant associations or environmental surrogates of biodiversity, implicitly assume that the different taxonomic elements of biological communities respond in the same way to the same environmental parameters and, thus, are similarly distributed (see Margules and Pressey, 2000). Recent work, including the WBS, has shown this is not true at the scale of a wetland or terrestrial site (McKenzie *et al.*, 2000; Davis *et al.*, 2001; Fleishman *et al.*, 2002). In part, this is the result of various organisms being distributed at different scales. Most manageable conservation units (such as a wetland and associated vegetation) are composed of mosaics of microhabitats, with the distribution of the biota being controlled within these microhabitats. For example, the relationship between wetland salinity and invertebrates is different from that between wetland salinity and plants, even for members of the same assemblage (Table 3), because most plants grow on the bank rather than in the water column. Wetland salinity values are often poorly correlated with soil salinity on the bank and, in fact, there is considerable variation in soil salinity on the bank according to small-scale topographical variation (Lyons *et al.*, 2004). The ability of waterbirds to move between wetlands means their distribution may not be fully determined by the characteristics of the wetland at which they were recorded. They may feed at a productive saline microhabitat, fly to a freshwater seep in another wetland to drink and roost in suitable microhabitat of a third wetland (Norman, 1983; see also Roshier *et al.*, 2001).

The varied responses of different taxa to their environment means that it is rare for one group of organisms to be an efficient surrogate for the occurrence of others at a site and, ideally, reserve selection should be based on surveys of all the biota (see Gaston, 2000). This was prevented by logistical constraints in the WBS, as is always likely to occur in broad-scale surveys. Nevertheless, the necessity of procedures for reserve (or in this case BRC) selection being explicitly based on a range of taxa was recognized and we surveyed aquatic invertebrates, waterbirds and plants. These elements operate at different spatial scales, have different life histories and represent both the waterbody and its surroundings. In terms of conservation and public interest, the riparian zone (or immediate surroundings of a wetland) is as important a habitat as the waterbody itself. The protection of terrestrial fauna species, including frogs, using the riparian zone was addressed in the WBS by McKenzie *et al.* (2004).

Reliability of survey patterns

One of the most significant issues with respect to the WBS is how well single surveys characterised wetlands and, therefore, whether the wetland types and species assemblages identified in this paper really reflect patterns of the wheatbelt and south coast. Reliability issues fall into two classes: (1) how well sampling reflected instantaneous community patterns, and (2) whether temporal variation in climate is likely to have affected patterns obtained. We use the term 'instantaneous' principally to refer to community composition during the season of sampling, although our testing of the invertebrate protocol also examined how well community composition at the actual time of sampling was documented.

Halse *et al.* (2002) examined the adequacy of invertebrate WBS sampling and analytical techniques to document patterns of instantaneous invertebrate communities. They were able to discriminate between communities of five basin wetlands along a salinity gradient. Given the static nature of vascular plants and the considerable survey effort used, it is likely that instantaneous community patterns of plants were also sufficiently well documented to characterise a wetland (Lyons *et al.*, 2004), although some species of submerged plants found in fresh water at the end of summer, some late-flowering herbs around claypans and *Ruppia* spp. (identification difficulties) were under-represented in the dataset. We undertook further analysis of some of Cale *et al.*'s (2004) waterbird and wetland data to show that, although waterbirds are highly mobile, instantaneous composition of waterbird communities can be characterised well enough by single surveys during spring, such as used in the WBS, to distinguish broad categories of wetland (Figure 11; see also Halse *et al.*, 2000a).

Large temporal fluctuations in wetland depth and salinity (both increases and decreases) sometimes cause substantial shifts in wetland communities. For example, the waterbird community at Lake Logue (SPM002) showed substantial differences between the dry year of 1997 when the lake was 0.36 m deep in spring and the wet years of 1999 and 2000 when it was *ca* 3 m (Figure 11, Table 6). On the other hand, Halse *et al.* (2000b) found the relationship between sites based on invertebrate samples remained constant across annual rainfall events in the southern Carnarvon Basin, and invertebrate and waterbird data collected in south-west Western Australia according to WBS protocols have shown a consistent relationship between wetlands across years when wetland conditions have been similar (Cale *et al.*, 2004; Figure 11). Similar results are likely for plants, with extreme flooding and very low water levels affecting communities substantially, but the communities remaining stable at intermediate water depths, except for minor rainfall-induced variation in the species composition of annual plants. Even annuals have adaptations to recruit at varying elevations depending on water depth in a given season, so that overall plant composition is relatively independent of the degree of flooding. The WBS plant sampling was designed to capture all zones of recruitment and minimise the effect of year on survey results (Lyons *et al.*, 2004).

Given that the northern wetlands were flooded beyond their usual boundaries and were less saline than usual when sampled in 1999, while wetlands surveyed in 1997 and 1998 in central and southern areas were experiencing dry, saline conditions (see Figure 2), it is possible that some long-term relationships between wetlands of the wheatbelt and south coast were obscured by rainfall patterns during the WBS by the kind of responses observed at Lake Logue (Figure 11). Extensive rainfall throughout the northern parts of Western Australia in 1999, at the same time as the northern wheatbelt was flooded, also allowed some tropical invertebrates to extend their ranges southwards to the wheatbelt (see Pinder *et al.*, 2004a). Some waterbird species (e.g. *Himantopus himantopus*) made the reciprocal movements and more-or-less disappeared from the wheatbelt (S.A. Halse and

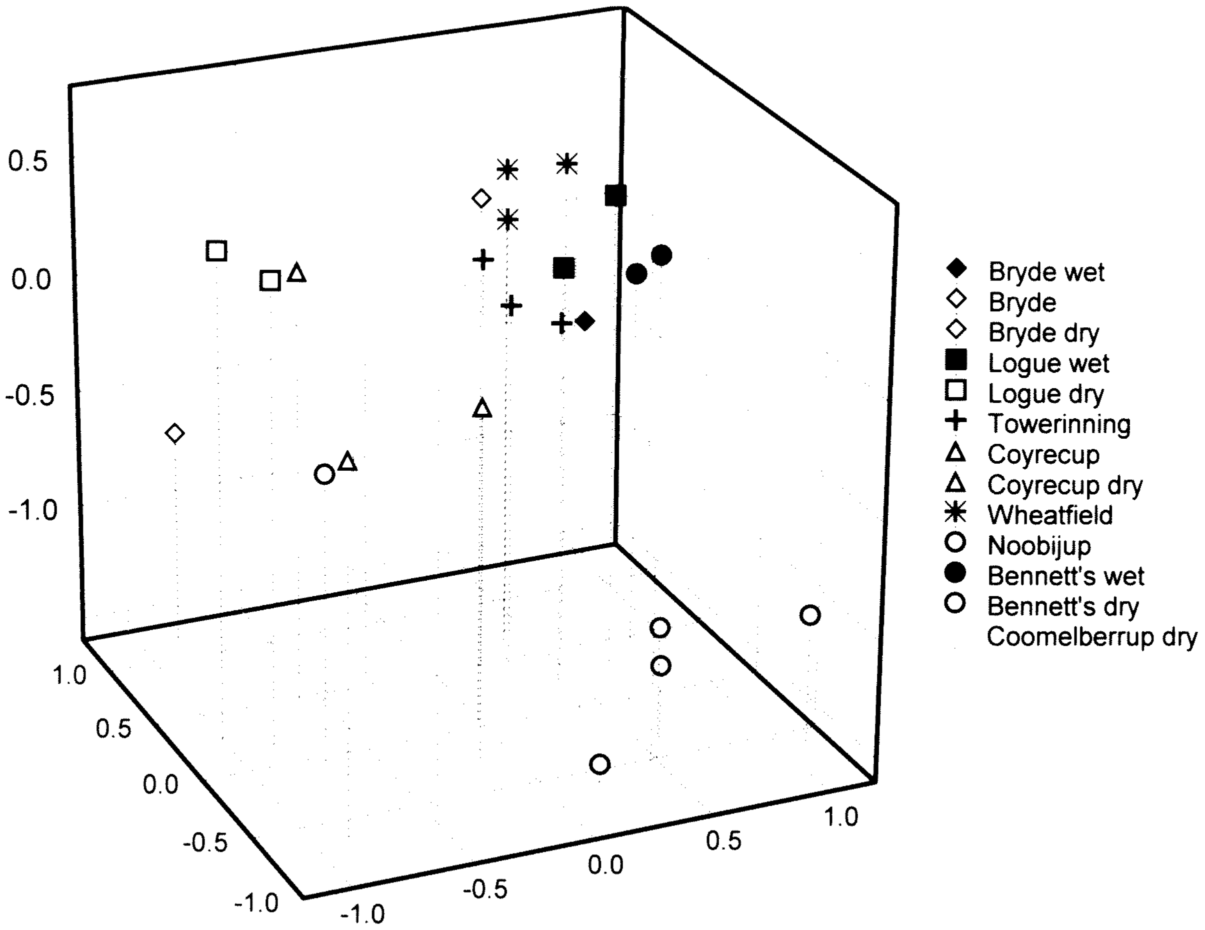

Figure 11 Ordination of waterbird communities at a series of wetlands surveyed in spring of different years (see Cale *et al.* 2004 for survey methods and Table 6 for information on wetland depths and salinities). Stress = 0.18.

G.B. Pearson unpublished data). Nevertheless, conditions at most northern wetlands in 1999 were probably not extreme enough to have had major impact on community characterisation and we suggest most of the WBS patterns are reliable.

Potential Recovery Wetlands

One of the major objectives of the WBS was to identify wetlands that might form parts of BRCs. The approach we adopted to identify PRWs is similar to that used by McKenzie *et al.* (1989, 2000) to identify conservation reserve requirements of terrestrial systems in the Nullarbor and southern Carnarvon Basin regions of Western Australia. They modelled the occurrence of each assemblage in the region of interest to provide the basis for selecting conservation areas in parts of the region that had not been surveyed. However, wetland assemblages are often poorly predicted by models (see Table 4) and only amenable to mapping as species richness isoclines when the assemblage is almost ubiquitous (see Figures 4–6). McKenzie *et al.* (2000) attempted to overcome these difficulties by basing conservation recommendations in the southern Carnarvon Basin on a wetland classification rather than on assemblages.

In the WBS, species assemblages were adopted as the units on which conservation measures would be based but a combination of modelling, fidelity analysis of species assemblages to wetland types, proportion of assemblages at species-rich sites and assemblage mapping have been used to form the basis for recommendations about conservation of assemblages and the wheatbelt biota. Summaries for each assemblage in terms of types of wetlands and areas where the assemblage is best represented, need for conservation, and the proportion of the whole assemblage likely to occur at any one site, are presented in Table 5. Where there is a need for conservation, we have suggested 1–3 surveyed wetlands or complexes that might be protected to conserve the assemblage. These PRWs should be regarded as indicative of the kinds of wetlands in need of protection; in many cases further survey may reveal wetlands supporting a higher proportion of the relevant assemblage. The notional percentage of each assemblage that would conserved by protecting the 19 PRWs, in addition to existing BRCs, in an otherwise salinised landscape varied between 42 and 100% (Table 5). This represents 72% of the waterbirds recorded during the WBS, 59% of the aquatic invertebrates

Table 5 Suggested focus for conservation of the various wheatbelt and south coast species assemblages. Preferred wetland types, part of the surveyed area where assemblage most common, sensitivity to salinisation, potential recovery wetlands (PRWs) and the maximum proportion of the assemblage present at individual wetlands are listed. The proportion of each assemblage that would be conserved (PC) by protecting the PWRs and existing Natural Diversity Recovery Catchments from salinisation is also shown.

Assemblage	Comments	PC
1	Type I and VIII wetlands, mostly in south-eastern wheatbelt and south coast with restricted occurrence, sensitive to salinisation, extends beyond wheatbelt, PRW Lake Cronin, proportion of assemblage at individual sites >0.5	0.67
2	Types I, II, III, IV, V, VI wetlands and rivers, widespread occurrence, some tolerance of salinisation, no special conservation requirement, proportion of assemblage at individual sites <0.3	0.42
3	Types IV, XI and XII rivers and wetlands, mostly on south coast with restricted occurrence, some tolerance of salinisation, PRW Lake Warden BRC, Oldfield River, proportion of assemblage at individual sites <0.3	0.44
4	Type VI rivers, mostly in wandoo woodland east of Perth, sensitive to salinisation, PRW Jimperding Brook, proportion of assemblage at individual sites <0.3	0.47
5	All fresh or sub-saline wetland and river types, widespread occurrence, sensitive to salinisation, no special habitat requirement, proportion of assemblage at individual sites >0.5	0.97
6	All wetland types except some very fresh and some hypersaline ones, widespread occurrence, tolerant of salinisation, no special habitat requirement, proportion of assemblage at individual sites >0.5	1.0
7	A plant-dominated assemblage, most of which are weeds, no special habitat requirement	0.87
8	Most fresh or sub-saline wetland and river types, mostly on south coast and higher rainfall parts of wheatbelt, sensitive to salinisation, no special habitat requirement, proportion of assemblage at individual sites <0.3	0.81
9	Types IV, XI and XII rivers and wetlands, mostly on south coast, moderately restricted occurrence, some tolerance of salinisation, PRW Lake Warden BRC, Oldfield River, proportion of assemblage at individual sites 0.3–0.5	0.97
10	Types XIII and XIV wetlands, mostly in eastern wheatbelt, some tolerance of salinisation, PRW Isthmus Lake, Lake Altham, Kondinin Samphire Marsh, proportion of assemblage at individual sites <0.3	0.64
11	Type XV wetlands, in north-eastern wheatbelt, sensitive to salinisation, PRW Lake Moore, Weelhamby Lake, proportion of assemblage at individual sites 0.3–0.5	0.80
12	Stronger affinity to northern and eastern wheatbelt than to wetland type, probably sensitive to salinisation, no special conservation requirement other than wetland in north-eastern wheatbelt (PRW Wannara Claypan), proportion of assemblage at individual sites <0.3	0.48
13	Type X and other saline/hypersaline wetlands, widespread occurrence, tolerant of salinisation, no special habitat requirement, proportion of assemblage at individual sites 0.3–0.5	0.91
14	Type XV wetlands, mostly in north-eastern wheatbelt, sensitive to salinisation, PRW Buntine-Marchagee BRC, Weelhamby Lake, proportion of assemblage at individual sites >0.5	0.97
16	Types VII and IX wetlands, mostly south-east of wheatbelt, sensitive to salinisation, PRW Youlabup Swamp, Ngopitchup Swamp), proportion of assemblage at individual sites <0.3	0.73
17	Type IX wetlands, western edge of wheatbelt, sensitive to salinisation, PRW Nalyerin Lake, Lake Muir BRC, proportion of assemblage at individual sites <0.3	0.93
18	Type IX wetlands, south-western edge of wheatbelt, sensitive to salinisation, PRW Lake Muir BRC, Nalyerin Lake, proportion of assemblage at individual sites 0.3–0.5	0.95
20	Types VII and VIII wetlands, patchy occurrence throughout wheatbelt, sensitive to salinisation, PRW Punjerwerry Claypan, proportion of assemblage at individual sites 0.3–0.5	0.82
21	Type VII wetlands, granite rock outcrops in eastern wheatbelt, protected from salinisation, PRW Wannara Rock, Dunn Rock, proportion of assemblage at individual sites 0.3–0.5	0.66

and 55% of the plants based on single surveys. When additional data from some PRWs and BRCS that had been sampled on multiple occasions were included in the analysis, 93% of waterbirds were sometimes found in the protected wetlands (see Cale *et al.*, 2004).

The above two estimates of waterbird protection afforded by PRWs demonstrate that levels of protection estimated in Table 5 need qualification. Firstly, on the positive side, some assemblages are unlikely to be threatened by salinisation. This is most obviously true for assemblages 6 and 21. The former consists of widespread salt-tolerant species that occur everywhere, including salinised

Table 6 October depth and salinity (electrical conductivity) in different years at eight wetlands in the Wheatbelt where waterbird communities were monitored (Cale *et al.* 2004).

	Year	Depth (m)	Salinity (mS cm^{-1})
Lake Bryde	1997	1.74	2540
	1999	0.05	53700
	2001	0.48	9510
Bennett's Lake	1998	0.6	1865
	2000	2.43	3810
	2001	2.95	2770
Lake Coomelberrup	1998	0.3	32800
	2000	N/A	91300
	2002	0.05	160900
Lake Coyrecup	1997	0.9	56100
	1999	1.09	56800
	2001	0.35	125000
Lake Logue	1997	0.36	12040
	1999	3.65	1929
	2000	2.52	3390
	2002	0.28	35700
Noobijup Swamp	1998	0.7	3800
	2000	N/A	3810
	2002	0.8	5700
Lake Towerinning	1997	3.19	9060
	1999	3.34	9300
	2001	2.37	16880
Lake Wheatfield	1997	2.0	10900
	1999	2.5	9010
	2001	1.92	9080

wetlands, and it was the only assemblage fully protected by the suggested 19 PRWs. Assemblage 21 is the least salt-tolerant assemblage but occurs in a habitat (granite rock outcrops) that will not become salinised (Pinder *et al.*, 2000).

Secondly, BRCs will nearly always contain a greater array of wetlands than we have sampled and, consequently, will support a greater proportion of some assemblages than the PRWs with which they are associated. For example, the Lake Muir BRC contains *ca* 100 wetlands, of which we sampled three. Twenty-seven Muir wetlands were sampled two or three times each in 1996–97 and yielded 488 invertebrate species (A.W. Storey, R.J. Shiel and S.A. Halse unpublished data) compared with 228 from the WBS sampling. Similarly, the Lake Bryde and Buntine-Marchagee Recovery Catchments support some freshwater wetlands we did not sample, as well as a large number of small salt pans in braided palaeochannels, and are likely to support more species than WBS data suggest. In addition to extra wetlands providing different habitat and extra species, annual variation in wetland conditions usually causes the long-term species list of a wetland to be greater than instantaneous lists (e.g. Halse *et al.*, 1993b; Timms, 1998). Provided sources of colonization exist, or propagules remain at the wetland, PRWs may help achieve conservation of more plant and invertebrate species than the analyses herein suggest.

A third, somewhat negative, consideration is the achievability of complete protection in recovery catchments. Some PRWs are likely to become degraded despite attempts to control salinity (Clarke *et al.*, 2002) and assemblage members relying on these wetlands may be lost (Halse *et al.*, 2003). However, the figures presented here on future protection of the biota relate only to the surveyed area and many species deemed to be at risk also occur in regions without a salinity threat. For example, the blue-billed duck *Oxyura australis* occurs on the Swan Coastal Plain (as well as in eastern Australia), the copepod *Calamoecia attenuata* and mayfly *Tasmanocoenis tilyardi* are widespread through southern Western Australia, the sedge *Baumea articulata* is widespread in coastal freshwater wetlands across southern Australia, and the chenopod *Tecticornia verrucosa* grows wherever suitable habitat occurs throughout Western Australia. Loss of these species from the wheatbelt will not cause extinction.

Rare species

Our analysis of the level of protection afforded to the aquatic biota by PRWs ignores singleton species, which comprised 34% of the biota. While some singletons have considerable conservation significance, many are not localised, rare species. The occurrence of many singletons on the edge of the surveyed area (Figure 10) suggests their apparent rarity is a sampling artefact. The steep rainfall gradients to the west and south of the study area cause considerable turnover in the biota over short distances (Hopper, 1979), which can be expected to lead to frequent occurrence of singletons in surveys. The invertebrate singletons in the northern wheatbelt were mostly tropical species that had extended south in a wet year (Pinder *et al.*, 2004).

Even within the main body of the study area, where the highest proportion of singletons requiring special conservation focus would be expected to occur, most singeletons do not warrant protection. Many plant singletons were species that occurred commonly at higher elevations in terrestrial habitats around wetlands. Only 5% were Priority Taxa (see Coates and Atkins, 2001) that, along with the single Specially Protected waterbird (*Botaurus poiciloptilus*), will require special conservation focus. Some of the 20% of singleton invertebrates that were new species or appeared to be localised (Pinder *et al.*, 2004a) will also require conservation focus, although many are likely to be found more widely after further survey.

Many of the rare plants, and some rare invertebrates, occurred in naturally saline wetlands.

In most cases, whether on private or public land, these wetlands were threatened with increased inundation because of salinisation. When salinisation is the principal threat, rare species usually cannot be protected through small-scale management actions aimed at the organisms and their immediate habitat (see Coates and Atkins, 2001). Catchment-scale solutions (Clarke *et al.* 2002) or very expensive localised engineering works (Froend *et al.*, 1997) are required.

Integrating wetland and upland protection

This paper has focussed on protecting biodiversity associated with wetlands which, because they are low in the landscape, are disproportionately threatened by salinisation (Halse *et al.*, 2003). However, protection of upland biodiversity is equally important and BRCs cannot be selected on wetland values alone. Results from terrestrial components of the WBS (McKenzie *et al.*, 2004) should be combined with recommendations about PRWs (Table 5) and species-rich examples of the identified wetland types (Figure 7) to identify catchments of 50,000–100,000 ha with particularly high biodiversity value. Irreplaceability analysis is one method of combining datasets of disparate biodiversity values and Walshe *et al.* (2004) have used the survey data to identify potential BRCs that encompass much of the biodiversity of the wheatbelt and south coast and provide the framework for landscape-scale conservation efforts.

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